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**Large Pelagic Fishes in the Caribbean Sea and Gulf of Mexico:
Current Status and Integrated Management**

**A Symposium Convened in Conjunction with
the 59th Annual Meeting of the
Gulf and Caribbean Fisheries Institute in Belize City, Belize
7 November 2006**



**GULF AND CARIBBEAN
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1000 N. ALA STREET, SUITE 100, TAMPA, FL 33604**

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Large Pelagic Fishes in the Caribbean Sea and the Gulf of Mexico: Current Status and Integrated Management

Mark S. Peterson

University of Southern Mississippi, mark.peterson@usm.edu

Nancy J. Brown-Peterson

University of Southern Mississippi, nancy.brown-peterson@usm.edu

James S. Franks

University of Southern Mississippi, jim.franks@usm.edu

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EDITORIAL COMMENTS

LARGE PELAGIC FISHES IN THE CARIBBEAN SEA AND GULF OF MEXICO: CURRENT STATUS AND INTEGRATED MANAGEMENT

A Symposium Convened on 7 November 2006 in conjunction with the 59th Annual meeting of the Gulf and Caribbean Fisheries Institute in Belize City, Belize.

Large pelagic fishes migrate throughout the Gulf of Mexico and Caribbean Sea and are widely harvested in commercial and recreational fisheries within the region. If overexploitation of the stocks of these transboundary species and the resulting negative impacts on fishers and user groups dependent upon them are to be avoided, sustainable utilization of large pelagics must be based on collaboration among countries in the context of regional management that is compatible with and functional within the existing management regimes. Fisheries management organizations are making some progress in addressing critical large pelagic fishery issues through various management initiatives, planning efforts, fishery management plans, and, in some instances, actual implementation of regulations (Mahon and McConney 2004, NMFS 2006). Regulation of large pelagic fishes that move across national boundaries is difficult and requires improved understanding of their biology and ecology in support of regional fisheries development and management. However, the development of management strategies to ensure the region-wide sustainability of large pelagic fish, fisheries, and user groups in the Gulf of Mexico and Caribbean Sea represents a complex process and requires input from fisheries scientists, resource managers and fishers.

The purpose of this symposium was to share current research on the biology and management of large pelagic fishes in the Caribbean Sea and Gulf of Mexico region and to develop a list of recommendations for future research and management of large pelagic fishes related to critical issues of regional concern. We wished 1) to initiate interactions and focused discussion among the GCFI participants on these vitally important issues through oral and poster presentations and a panel/audience discussion, 2) to produce a series of peer-reviewed papers on the current state of knowledge of large pelagic fishes in the Caribbean Sea and Gulf of Mexico, and 3) to allow the committee, based on these presentations and subsequent panel discussions, to develop a synthesis of critical issues of regional concern and the development of a list of recommendations pertaining to future research and management of large pelagic fishes in the region (Brown-Peterson et al., *this issue*). The symposium consisted of 2 keynote speakers (*B. Luckhurst*

and *E. Prince [for N. Thomsson]*), 3 invited theme speakers (*E. Prince, J. McDowell, and P. McConney*), and contributed oral and poster presentations. The Symposium Themes were 1) Fisheries Ecology, 2) Movements and Population Structure, and 3) Management: Strategies, Problems and Solutions. This Special Issue is organized around these 3 themes and comprised 45 total oral and poster presentations.

Papers presented under the Fisheries Ecology theme addressed a number of fundamental and applied topics ranging from basic reproduction (Arocha, *this issue*), abundance and distribution (Cortes et al., Fulling et al., *this issue*) to feeding behavior (Hoffmayer et al., *this issue*) and influences of hypoxia on habitat use (Prince and Goodyear, *this issue*). Papers presented under the Movements and Population Structure theme addressed both short-term (Loefer et al., Kraus and Rooker, *this issue*) and long-term (Luckhurst, *this issue*) movements of large pelagic fishes as well as a detailed analysis of the population structure of blue marlin (McDowell et al., *this issue*). Papers presented under the Management: Strategies, Problems and Solutions theme were diverse and ranged from local island fishing culture (Grant et al., *this issue*), description of a large-scale pelagic fish tagging study (Singh-Renton and Renton, *this issue*), and an overview of the US large pelagic fisheries (Thompson and Prince, *this issue*), to the changes in the fisheries catch in a Caribbean MPA (Castro et al., *this issue*), fishing mortality of sharks (Morgan and Burgess, *this issue*), eco-tourism of whale sharks (Graham, *this issue*) and an conceptual overview of management within the wider Caribbean Sea and Gulf of Mexico (McConney et al., *this issue*). Also included are the abstracts from papers presented in the symposium but not submitted for publication in this issue. Finally, the abstracts from other presentations given at the symposium are arranged by theme and presented at the end of this issue. Additionally, the abstracts from the peer-reviewed papers, as well as, full papers or abstracts of the other symposium presentations are also found in the 59th Proceedings of the Gulf and Caribbean Fisheries Institute.

Finally, in order to incorporate as many stakeholders as possible, we established a 5 member panel (*H. Oxenford,*

B. Luckhurst, A. Kinch, E. Prince, and L. Reynal) and a moderator (M. Haughton) from throughout the Caribbean and Gulf of Mexico regions. These individuals encapsulated a broad-based expertise and collectively had vast experience in large pelagic fisheries. Each panel speaker briefly addressed one or more of the following points at the beginning of the discussion: 1) Transboundary issues; 2) Conservation; and 3) Equity in fisheries (i.e., how to maintain equity when dealing with vast differences in the “scale” of economies, political power, fisheries authorities, and fishing/post-harvest enterprises among the various Gulf and Caribbean countries). This was followed by audience participation in the form of a ‘question and answer session’ which led to identification of 4 major issues related to large pelagic fishes as well as possible recommendations (Brown-Peterson et al., *this issue*).

The Symposium Organizing Committee consisted of Jim Franks, Nancy Brown-Peterson, Mark S. Peterson (all from The University of Southern Mississippi, USA), Peter Sheridan (National Marine Fisheries Service, Panama City, USA), Brian Luckhurst (Department of Environmental Protection, Bermuda), Hazel Oxenford, and Patrick McConney (both from the University of the West Indies, Barbados).

ACKNOWLEDGEMENTS

We thank the EXCOM of the Gulf and Caribbean Fisheries Institute (GCFI) and the myriad of sponsors (*see below*) without whose financial and technical support, this symposium would not have been possible. Specifically, B. Glazer and A. Acosta of the GCFI were vital in terms of logistics before, during and after the meeting. Additionally, the remainder of the symposium committee, B. Luckhurst, P. Sheridan, H. Oxenford, and P. McConney each played important roles in the organization, onsite logistics, and post-symposium ‘decompression.’ Their friendship and dedication is very much appreciated.

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EDITORIAL COMMENTS

**Peterson, Editor-in-Chief, Gulf and Caribbean Research,
Nancy J. Brown-Peterson, and James S. Franks¹**

Department of Coastal Sciences

¹*Center for Fisheries Research and Development*

Gulf Coast Research Laboratory

The University of Southern Mississippi

703 East Beach Drive

Ocean Springs, MS 39564

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Large Pelagic Fishes in the Wider Caribbean and Northwest Atlantic Ocean: Movement Patterns Determined from Conventional and Electronic Tagging

Brian E. Luckhurst

Department of Environmental Protection, Bermuda

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LARGE PELAGIC FISHES IN THE WIDER CARIBBEAN AND NORTH-WEST ATLANTIC OCEAN: MOVEMENT PATTERNS DETERMINED FROM CONVENTIONAL AND ELECTRONIC TAGGING

Brian E. Luckhurst

Marine Resources Division, Department of Environmental Protection, PO Box CR 52, Crawl CRBX, Bermuda, E-mail bluckhurst@gov.bm

ABSTRACT Conventional tagging data has documented long distance movements (including trans-Atlantic movements) in blue marlin (*Makaira nigricans*) and yellowfin tuna (*Thunnus albacares*) within the Atlantic. Swordfish (*Xiphius gladius*) have also been shown to move substantial distances, although primarily in a north-south direction. There is, however, a paucity of data for wahoo (*Acanthocybium solandri*). In the past several years, electronic archival (i.e., data recording) tags have significantly advanced our understanding of the behavior and movement patterns of large pelagic fishes. Data from electronic archival tags have generally corroborated conventional tagging data with respect to long distance movements, as well as the daily vertical movement patterns previously obtained through acoustic telemetry. Taken together, it is now possible to define “habitat envelopes” for pelagic species and to correct nominal catch rates for changes in gear vulnerability due to differences in gear targeting. In general, there is a broad spectrum of vertical movement patterns: blue marlin and yellowfin tuna generally remain within the uniform temperature surface layer (although blue marlin occasionally descend to below 300 m), wahoo have less vertical range and appear to remain above 50 m most of the time, whereas swordfish mirror the vertical movements of the organisms of the deep-scattering layer remaining within about 20–30 m of the surface at night but descending to 700–800 m during the day. Tagging data demonstrates that many large pelagic fish species move through the waters of other jurisdictions thus requiring a regional and international approach to assessment and management. The primary organization which undertakes this function in the Atlantic Ocean is the International Commission for the Conservation of Atlantic Tunas (ICCAT), which is responsible for the assessment and management of tunas, swordfish and billfishes.

INTRODUCTION

A world review of highly migratory species and straddling stocks (FAO 1994) provided a summary of the major fisheries for pelagic species in the world's oceans and their status. In the Atlantic, 5 species of tunas, billfishes and swordfish are listed as the principal species taken by pelagic longline fishing fleets. In the western North Atlantic, the majority of fishing effort for target species is by longliners while surface fisheries (purses seiners and baitboats) predominate in the eastern Atlantic (ICCAT 2006). In the wider Caribbean (including Bermuda), the majority of large pelagic species are taken by artisanal fleets principally by trolling. Despite their economic importance, relatively little is still known about the migratory patterns of the majority of these pelagic species. This lack of knowledge provided the impetus for tagging programs to be instituted to elucidate movement patterns. Understanding movement patterns is an important component of regional and international fisheries management programs.

The first tagging program in the Atlantic (the Cooperative Game Fish Tagging Program) was started in the USA in 1954 at Woods Hole Oceanographic Institute. An account of the origins and history of this program is provided by Scott et al. (1990). The program involves both recreational and commercial fishermen as well as scien-

tists for tag release and recovery activities of a wide range of fish species (Ortiz et al. 2003). An examination of the recapture results from this tagging program (now called the Cooperative Tagging Center (CTC) based at the National Marine Fisheries Service (NMFS) Southeast Fisheries Science Center (SEFSC) in Miami, Florida) indicate that many large pelagic fish species are highly migratory and can make trans-Atlantic crossings. This has been demonstrated in several species including blue marlin (*Makaira nigricans*) (Ortiz et al. 2003) and yellowfin tuna (*Thunnus albacares*) (E. Prince, pers. comm., NMFS, Miami, FL). Tagging effort for blue marlin has been concentrated in the NW Atlantic and, since the 1980s, there has been a growing conservation ethic in the recreational billfish fishery which has resulted in increased tagging effort. The Billfish Foundation (TBF) has actively promoted tagging as part of catch and release fishing for billfish since 1990 (Ortiz et al. 2003).

In recent years, the development of sophisticated electronic tags has helped reveal the migration tracks of the species, the speed at which they move, and vertical habitat use. The first dedicated electronic tagging program for large pelagics was directed at bluefin tuna (*Thunnus thynnus*), a highly important species in the North Atlantic and Mediterranean Sea due to strong market demand for sushi-grade tuna. The results of multi-year tagging of bluefin

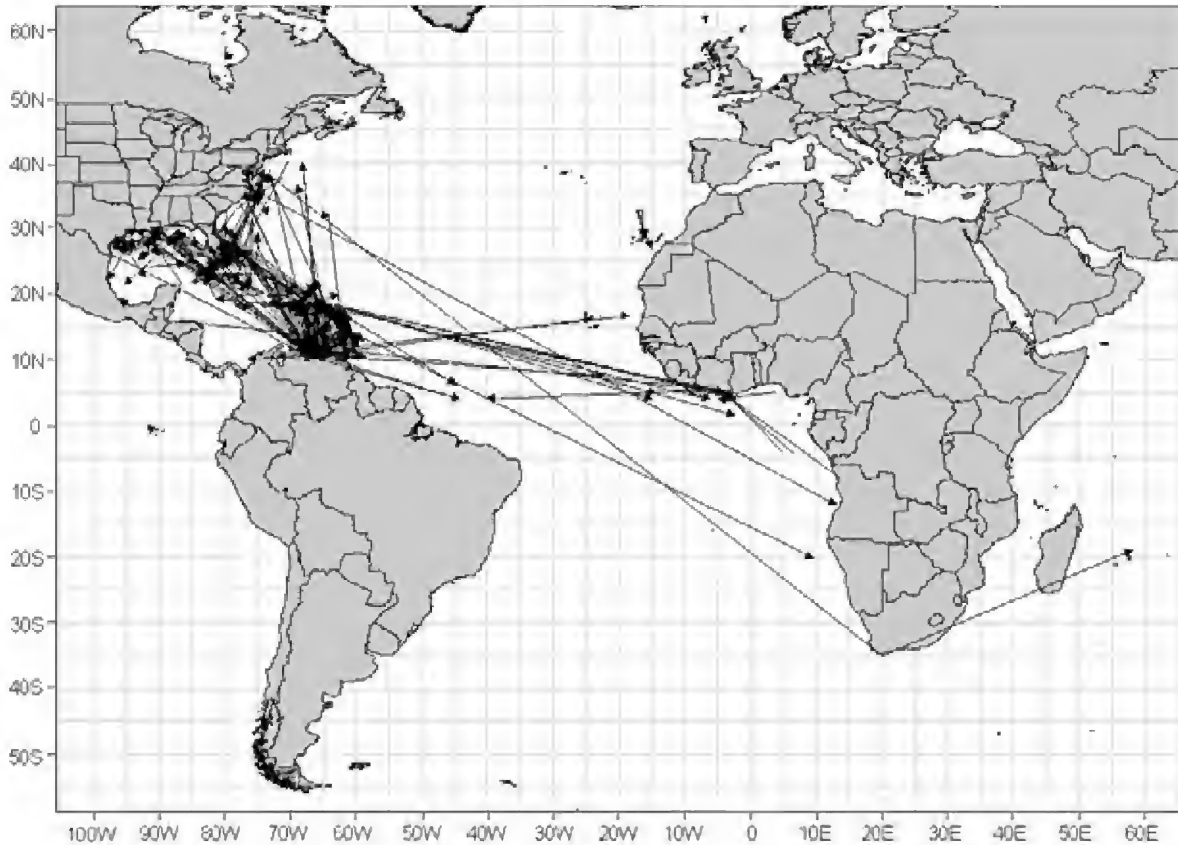


Figure 1. Movement vectors of conventionally-tagged blue marlin (*Makaira nigricans*) in the North Atlantic from 1974-2006. Note number of trans-Atlantic crossings.

tuna have documented numerous trans-Atlantic crossings (Block et al. 2001). The deployment of PSATs (Pop-up Satellite Archival Tags) on blue marlin in the Northwestern Atlantic, primarily through the Adopt-A-Billfish Program, started in 1999 (E. Prince, pers. comm., NMFS, Miami, FL) has revealed extensive movements in relatively short time periods. The tagging of other large pelagic species with PSATs has also been undertaken in the past few years. For example, Sedberry and Loefer (2001) deployed PSAT tags on swordfish (*Xiphius gladius*) off the coast of South Carolina and more recently, Thiesen and Baldwin (In press) PSAT-tagged wahoo (*Acanthocybium solandri*) in the Bahamas. To date, results from these deployments also indicate extensive movements. I have chosen 4 species from 3 separate families, common in the NW Atlantic, to illustrate the scale of movements documented in large pelagic species:

- 1) Blue marlin—primarily a target species of the recreational fishery in the Western Atlantic but with commercial (artisanal) fisheries off West Africa.
- 2) Swordfish—exclusively a commercial species taken Atlantic-wide by longliners. Harpoon fisheries for this species have been in decline for some years.

3) Yellowfin tuna—a commercial species Atlantic-wide but with considerable recreational importance in the NW Atlantic.

4) Wahoo—a commercial species in the wider Caribbean but with growing recreational significance in the NW Atlantic.

The focus of my paper is regional, emphasizing data from the wider Caribbean and the Gulf of Mexico (GOM). Thus, references to tagging studies in other oceans are limited. I will examine movement patterns, as revealed by both conventional and electronic tagging, at 2 geographic scales: 1) NW Atlantic and 2) around Bermuda.

In particular, I will attempt to illustrate how these movement patterns provide strong evidence for connectivity between different parts of the Atlantic and why this information is important for regional and international fishery management agencies. I will also illustrate how the data from PSATs has provided invaluable insights into vertical habitat use by blue marlin and swordfish.

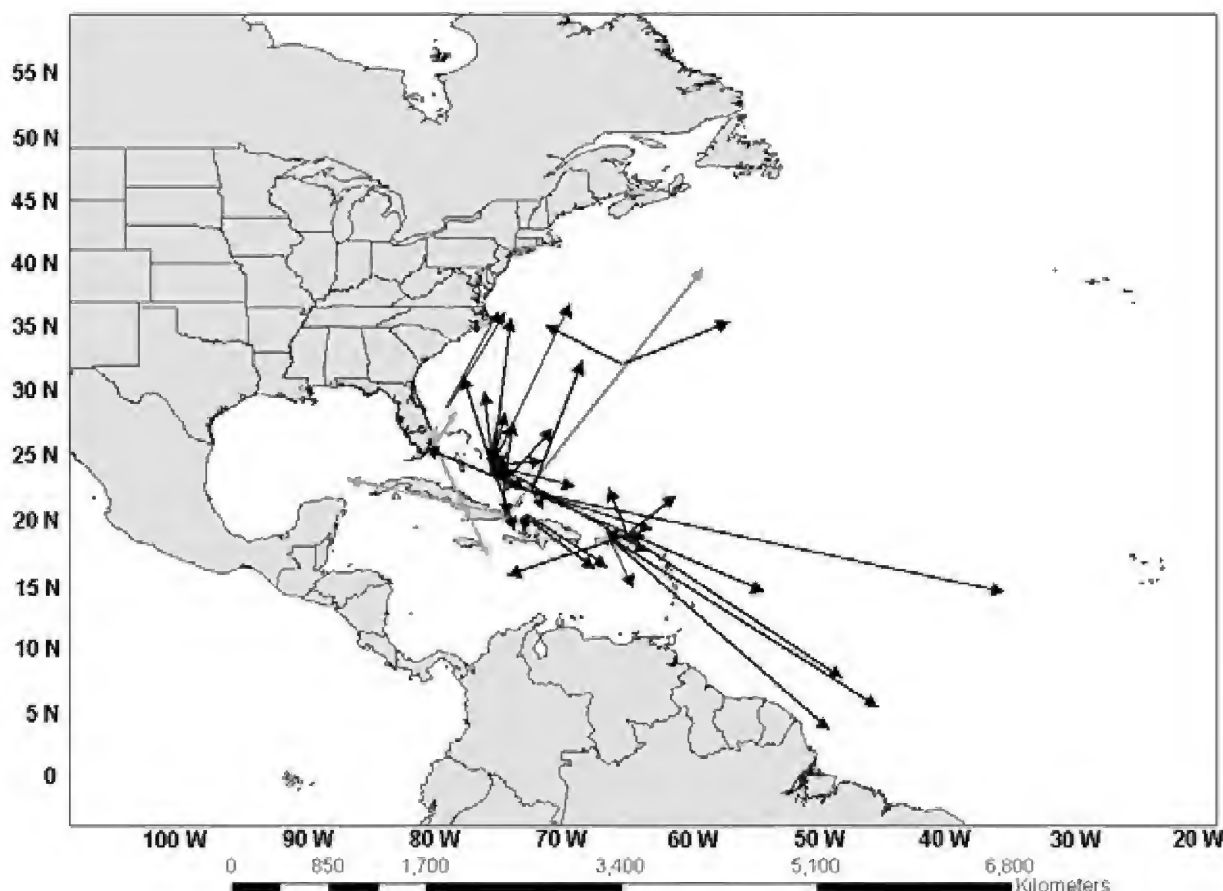


Figure 2. Movement vectors of blue marlin (*Makaira nigricans*) [dark vectors] and swordfish (*Xiphius gladius*) [pale vectors] tagged with Pop-up Satellite Archival Tags (PSATs) in the western North Atlantic from 2002–2006.

RESULTS

Blue marlin

An examination of the databases (CTC and TBF) of conventional tag deployments on blue marlin indicates that the majority of tagging effort has taken place in the western Atlantic (Ortiz et al. 2003). There have been a total of 52,185 blue marlin releases and 769 recaptures as of the end of calendar 2005, with 18 of these recaptures demonstrating trans-Atlantic movements (E. Prince, pers. comm., NMFS, Miami, FL). Tag recapture rates for blue marlin are generally < 1% throughout the world's oceans; the specific recapture rates for the NW Atlantic are: CTC = 0.91%, TBF = 1.74% (Ortiz et al. 2003). The dominant movement patterns for recaptured fish are primarily from west to east and, as blue marlin favor tropical waters, these movements are primarily in the tropical Atlantic (Figure 1). The longest documented movement of a blue marlin (1,108 d at large) was from Delaware, USA to Mauritius in the Indian Ocean (Figure 1), a distance of 14,893 km (Ortiz et al. 2003).

The first PSAT tagging of blue marlin in the NW Atlantic took place in the recreational fishery in Bermuda in 1999 (Luckhurst, pers. obser.). Eight of the 9 tagged blue marlin reported their positions after 5 days and moved distances ranging from 73.8–248.6 km but in all compass directions (Graves et al. 2002). Longer deployments of PSAT tags on blue marlin from commercial longliners in the NW Atlantic demonstrated substantial movement distances (Kerstetter et al. 2003). Two blue marlin tagged with PSATs moved distances of 985 km and 1,968 km in 30 d. During the period 2002–2003, a total of 66 PSATs were deployed (E. Prince, pers. comm., NMFS, Miami, FL), primarily from recreational fishing vessels in the wider Caribbean. These deployments resulted in long distance movements by a number of specimens (Figure 2). The longest movement vector of 4,606 km was of a blue marlin (68 kg) tagged in the Turks and Caicos Islands in 2003 which moved this distance to the eastern tropical Atlantic in 91 d (Figure 3). A detailed analysis of the satellite-transmitted data for this fish indicates that over 40% of its time was spent in the top 25 m of the water column although it made several dives to below 300 m depth

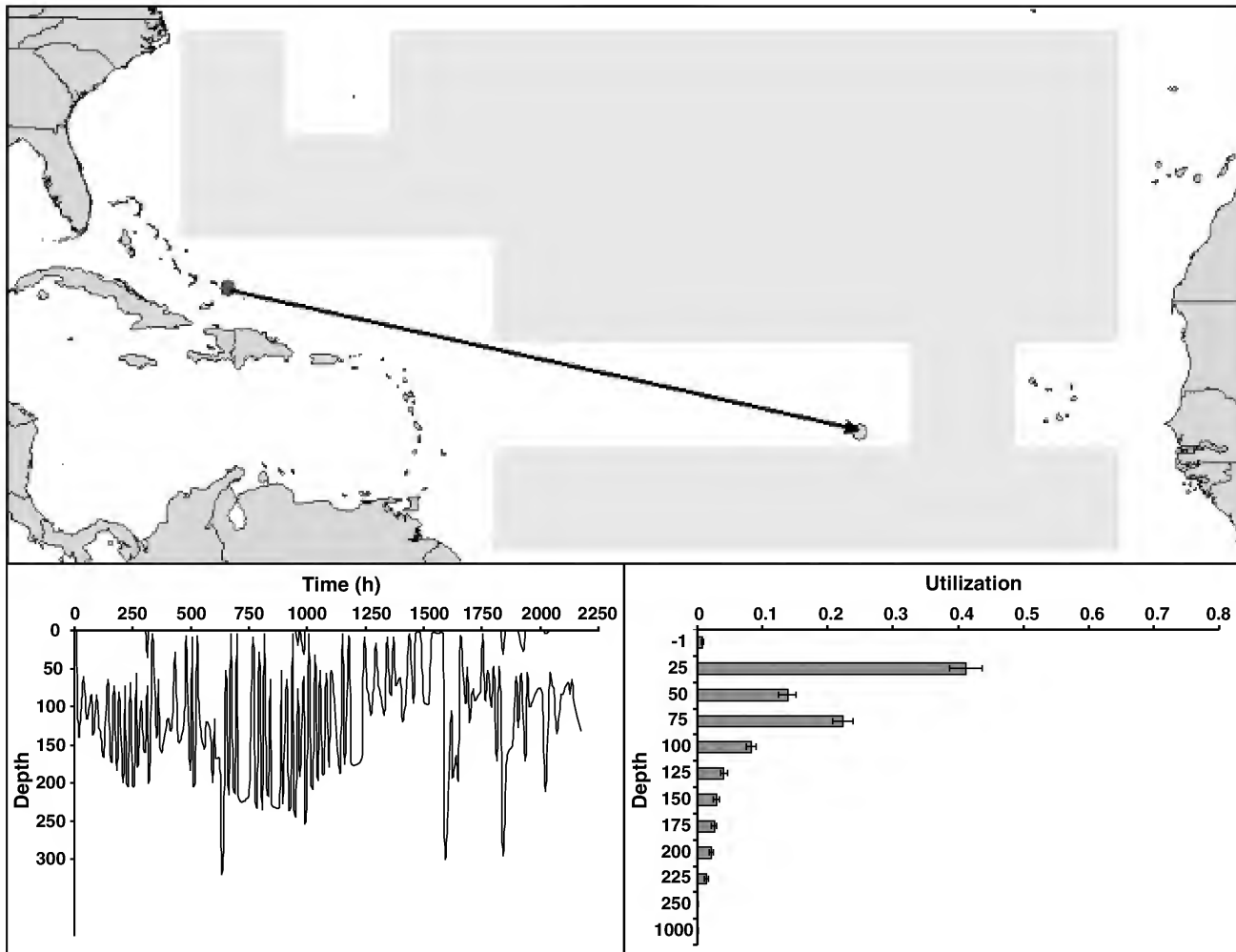


Figure 3. Movement vector of single blue marlin (*Makaira nigricans*), estimated at 68 kg, tagged with a PSAT, which moved 4,606 km in 91 d. From insets note that the largest proportion of time ($\bar{x} \pm s_x$) is spent in < 100 m depth.

(Figure 3). Several other blue marlin tagged in the northern Caribbean moved considerable distances to an area off the coast of Brazil (Figure 3).

Swordfish

Conventional tagging of swordfish has taken place since the late 1950s due to its commercial importance and virtually all of the tagging effort has occurred in the western Atlantic and GOM. As of the end of 2006, a total of 10,767 swordfish have been conventionally tagged with 395 recaptures (E. Prince, pers. comm., NMFS, Miami, FL). The predominant movement pattern of tag-recaptured swordfish in the western Atlantic appears to be north-south (Figure 4) although some east-west movement is also evident, including several trans-Atlantic movements. A swordfish conventionally-tagged from a longliner in the NW Atlantic in July 1997 moved in a southerly direction > 900 km before being recaptured off Bermuda in

December, <6 months later (Luckhurst, pers. obser.; E. Prince, pers. comm., NMFS, Miami, FL).

A relatively small number of PSAT tags have been deployed on swordfish in the NW Atlantic ($N < 40$, E. Prince, pers. comm., NMFS, Miami, FL). The movement vector of a swordfish (59 kg) tagged with a PSAT tag in the Windward Passage in 2004, indicates a northerly movement of 2,629 km in 62 d (Figure 5). Throughout the monitoring period, this fish made regular dives to 700–800 m depth during daylight hours (Figure 5). During nocturnal hours, mean depth was much shallower but brief, regular periods were spent at the surface (Figure 5).

Yellowfin tuna

In common with blue marlin and swordfish, the great majority of conventional tagging effort has occurred in the western Atlantic, primarily off the eastern seaboard of the US and, to a lesser extent, in the GOM. There have

MOVEMENT OF LARGE PELAGIC FISH

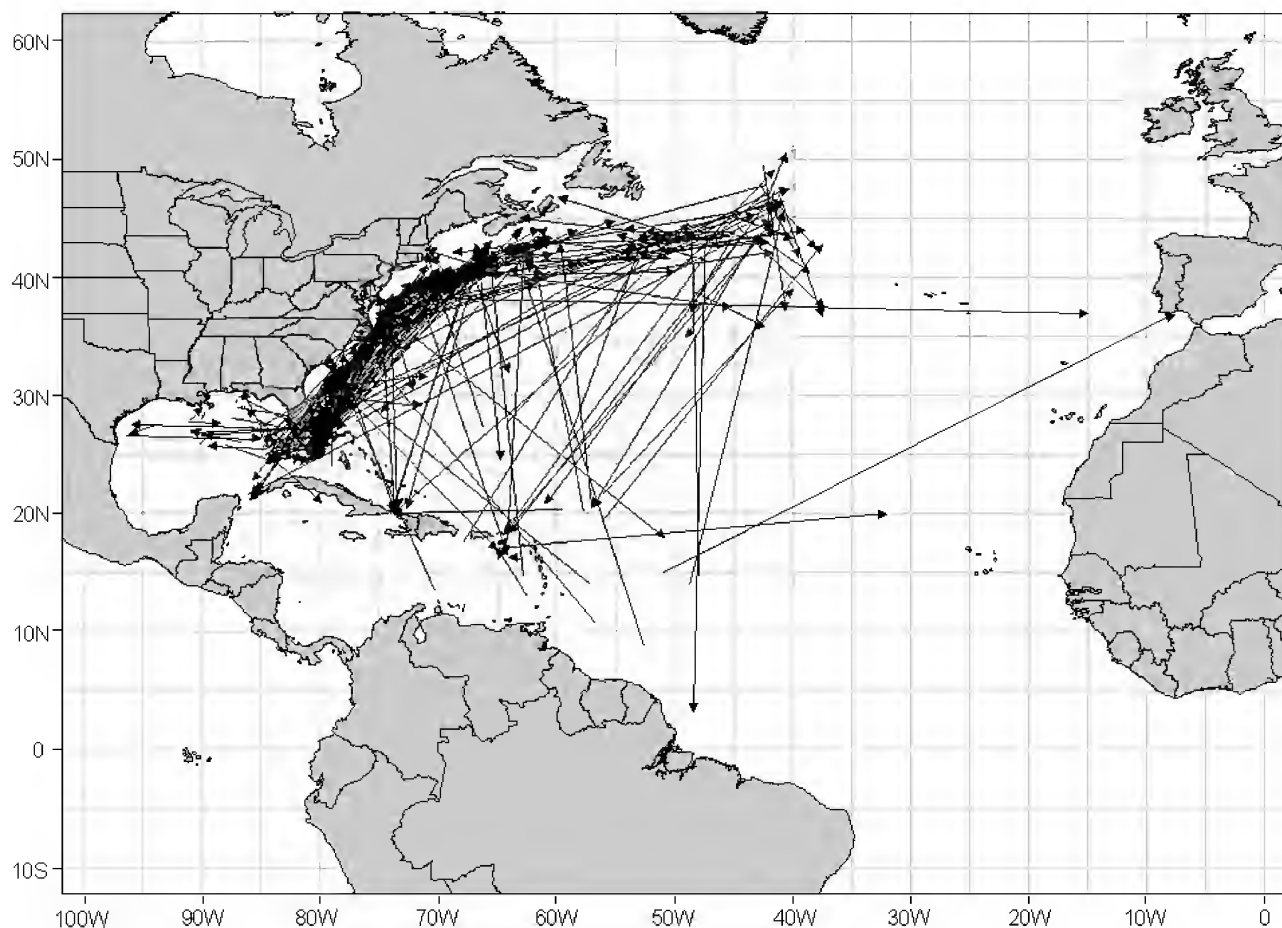


Figure 4. Movement vectors of conventionally-tagged swordfish (*Xiphius gladius*) in the North Atlantic from the CTC database until end of 2006. Note predominantly north-south movements.

been 10, 448 yellowfin conventionally-tagged up until the end of 2006 (E. Prince, pers. comm., NMFS, Miami, FL). Tag-recapture results indicate a strong west to east movement from most tagging locations to the vicinity of the Gulf of Guinea off west Africa (see Prince and Goodyear, this volume, their Figure 3). To a lesser extent, there was also southerly movement from off the US eastern seaboard toward the Caribbean and also within the GOM. Despite this strong migratory tendency, acoustic tagging of yellowfin around oil platforms in the GOM has demonstrated that yellowfin can be resident or seasonally resident within a limited area (Edwards and Sulak 2006).

An examination of movements of conventionally-tagged fish on a limited geographic scale, e.g., around Bermuda, can provide useful insights. To date, there have been a total of 574 yellowfin tuna tagged in Bermuda coastal waters. There have been 91 recaptures of Bermuda-tagged fish for an overall recapture rate of 15.9%. However, only 3 recaptures (3.3%) were outside Bermuda waters (E. Prince, pers. comm., NMFS, Miami, FL). Two recaptures

were off the coast of Puerto Rico and the other was near Cape Hatteras (Figure 6). These 3 fish moved distances of 1,000–1,300 km illustrating connectivity of Bermuda with the larger NW Atlantic region.

An analysis of yellowfin tuna tag-recapture patterns around Bermuda can provide estimates of residence time around the Bermuda Seamount and insights into possible movement patterns. A selection of Bermuda recapture data from the CTC database (Table 1) illustrates the utility of using conventional tagging data. Short term periods at liberty provide an estimate of residence times and longer term periods (on the order of a year) suggest the use of the Bermuda Seamount on a seasonal migratory route in the NW Atlantic (Table 1).

Wahoo

Little is known about wahoo movement patterns in the western North Atlantic Ocean because few tagging programs have targeted wahoo. A program in the SE Caribbean tagged a total of 250 fish but there have been

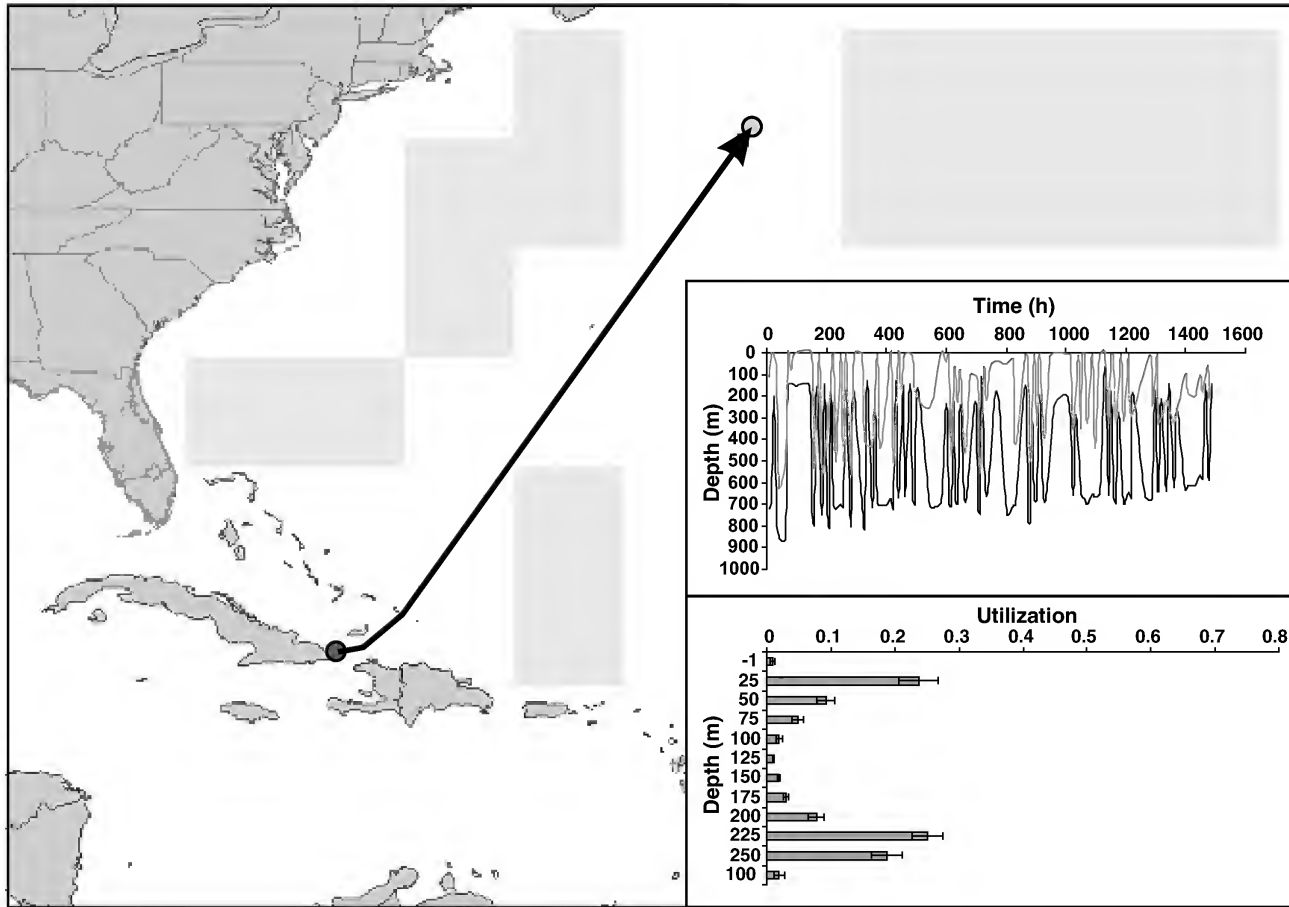


Figure 5. Movement vector of single swordfish (*Xiphius gladius*) estimated at 59 kg, tagged with a PSAT, which moved 2,629 km in 62 d. Inset: Note the number of dives to depths of 700 m or greater and bimodal distribution of time-at-depth (mean \pm s_x) reflecting diurnal vertical migration.

no recaptures to date (Singh-Renton 2006). Similarly, the CTC database indicates that a total of 159 wahoo have been tagged but there have also been no recaptures (E. Prince, pers. comm., NMFS, Miami, FL). A small-scale tagging program ($N = 15$) in Bermuda, using a specially-designed tagging cradle for wahoo (Nash et al. 2002), resulted in one recapture after 10 months at liberty. The recapture location was at Challenger Bank, a minimum distance of 65 km from the release site; however, this single recapture provides little insight into the distance actually moved during the time at liberty.

Tagging of wahoo with PSATs has begun only recently and initial results from 3 tagged fish in the NW Atlantic suggest that wahoo move considerable distances (Thiesen and Baldwin In press). The movement patterns of these tagged fish appeared to be largely north-south movements in relation to the Gulf Stream. One tagged fish moved 580 km in 54 d. Satellite-transmitted data from another wahoo, moving along the western edge of the Gulf Stream, indicated that it spent most of its time in the depth range

20–120 m, with almost daily trips to the surface and regular dives to almost 200 m. However, it rarely went below this depth. It also reportedly stayed in a relatively narrow temperature range (20–25°C).

DISCUSSION

The movement data presented here provide convincing evidence that the 4 large pelagic species illustrated in this paper all undertake extensive movements or migrations. Both blue marlin and yellowfin tuna are shown to commonly make trans-Atlantic movements. Similar long-distance movements are also documented for swordfish. The database for wahoo tagging is limited but recent results appear to suggest extensive movements as well (Thiesen and Baldwin In press). The movement patterns of these species demonstrate connectivity between different regions of the Atlantic Ocean.

The scale of demographic connectivity in pelagic fish populations is generally not well known but important

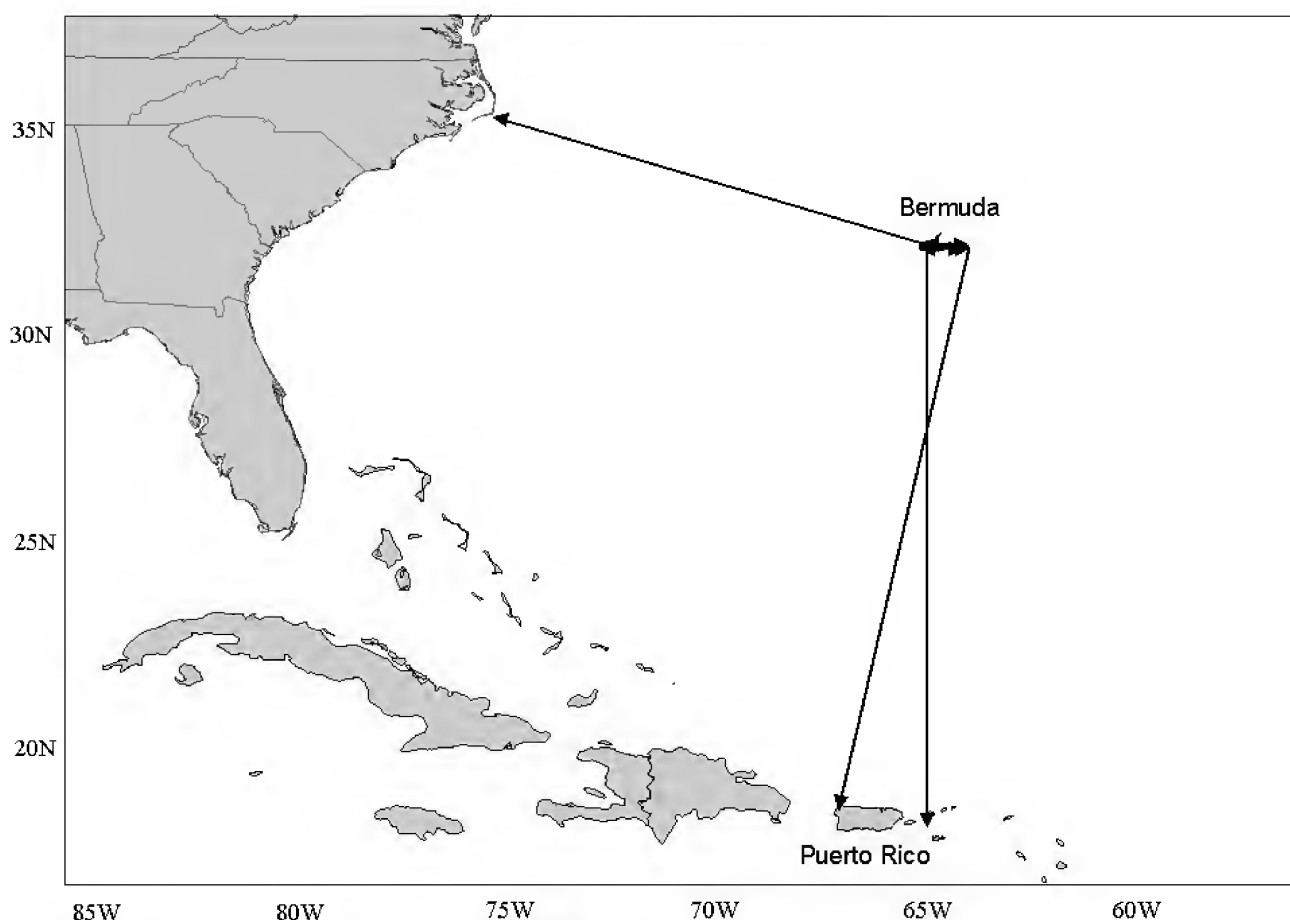


Figure 6. Movement vectors of three conventionally-tagged Bermuda yellowfin tuna (*Thunnus albacares*) recaptured outside Bermuda coastal waters demonstrating demographic connectivity with the wider Caribbean and US eastern seaboard. Distances moved were between 1,000 and 1,300 km.

insights may be gained using metapopulation concepts which examine changes in population size, age structure and genetic structure (Kritzer and Sale 2004). A number of factors such as larval dispersal potential (Cowen et al. 2006) and spawning site fidelity (Fromentin and Powers 2005) must be evaluated in determining demographic connectivity. The demonstrated scale of movement of the species presented here confirms the need for the management of these highly migratory species by international fishery management agencies. The ICCAT currently regulates the fisheries for pelagic species for its 43 members (contracting parties) having management measures in place for blue marlin, yellowfin tuna and swordfish. However, wahoo, which is included in the small tunas category at ICCAT, is not currently managed. The US is the only jurisdiction which currently has a management plan for wahoo (SAFMC 2004).

Blue marlin

The results of conventional tagging of blue marlin clearly demonstrate that they make trans-Atlantic and trans-equatorial movements. One fish made an inter-ocean movement from the Atlantic to the Indian Ocean (Ortiz et al. 2003). The advent of electronic tagging of blue marlin, particularly since 1999, has provided a wealth of data which has allowed insights into aspects of habitat use which were not possible with conventional tag-recapture data. Kerstetter et al. (2003) found that 2 blue marlin tagged with 30-d PSATs in the NW Atlantic spent the great majority of their time (65.4% and 81.5%) in the upper 5 m of the water column. The integration of detailed temperature-depth-time data from PSAT tagging allows for the definition of “habitat envelopes” (Luo et al. 2006). The use of “habitat envelopes” in conjunction with studies of fishing gear behavior, e.g., pelagic longlines (Luo et al. 2006), can provide important insights into the interaction between fish and fishing gear. This can lead to modifications of fishing strategy and gear deployment which may

TABLE 1

Selection of tag-recapture results of yellowfin tuna (*Thunnus albacares*) from the Cooperative Tagging Center database, Miami. All data presented are for fish tagged and recaptured at Challenger Bank, Bermuda and indicate the inferences which could be drawn from the days-at-liberty.

Tag No.	Tagging Date	Recapture Date	Days-at-liberty	Inference
R294318	24-May-93	8-Jun-93	15	residence time
R199052	24-May-93	9-Jun-93	16	residence time
R199053	24-May-93	11-Jun-93	18	residence time
R199054	24-May-93	19-Jun-93	26	residence time
R120387	26-May-93	8-Jul-93	43	residence time
R058096	3-Jul-83	8-Jun-84	340	migration route
R058100	3-Jul-83	5-Jul-84	367	migration route
R058102	3-Jul-83	17-Jul-84	379	migration route
R058154	4-Jul-83	19-Jul-84	380	migration route
R058151	4-Jul-83	28-Jul-84	389	migration route
R018715	9-Jul-83	6-Jun-84	332	migration route

help to reduce the level of fishing mortality on by-catch species such as blue marlin.

Swordfish

The reason for the predominantly north-south movements of swordfish in the western Atlantic as generated from conventional tagging is unclear, although it may be associated with seasonal changes in oceanographic productivity. However, it is known that higher densities of swordfish are associated with oceanographic features such as thermal boundaries between water masses where prey species may be more concentrated. These oceanographic features are dynamic systems with low levels of predictability. Sedberry and Loefer (2001) demonstrated that swordfish PSAT-tagged ($N = 29$) in the vicinity of the Charleston Bump moved considerable distances mainly in an E-NE direction. The longest movement documented was 2,497 km. They also determined that these tagged fish were often associated with offshore seamounts or the thermal boundaries of the Gulf Stream. Takahashi et al. (2003) deduced the movements of a PSAT-tagged swordfish off the east coast of Japan by comparing water temperature data from the archival tag with oceanographic data. They showed that the fish moved in a cyclic seasonal pattern between summer and winter periods. In contrast to horizontal movements, tracking vertical movements in the water column generally has more precision as water column structure is more predictable. The pattern of vertical habitat use exhibited by swordfish derived from PSAT tagging indicates that swordfish spend the majority of nocturnal hours in warmer, surface waters where they are vulnerable to longline fisheries. During daylight

hours, they make dives to 700–800 m on a regular basis. A swordfish tagged off Japan made a dive to a maximum depth of over 900 m (Takahashi et al. 2003). The bimodal pattern of vertical habitat use is believed to be associated with diurnal vertical migration which is probably linked to feeding periodicity. It is also linked to metabolic needs as water temperatures at depth are cold and swordfish are thought to spend nocturnal hours in surface waters to warm up after excursions to depth.

Yellowfin tuna

Conventional tagging of yellowfin tuna, since the early 1960s, has been conducted in the western Atlantic, primarily by recreational fishermen (E. Prince, pers. comm., NMFS, Miami, FL). Although recreational fishing effort has increased over the past few decades, yellowfin tuna are taken mainly by industrial fisheries. Tag recaptures usually reflect where the fishery is most intensive and, in the Atlantic, the major fishery is the purse seine fishery in the Gulf of Guinea (ICCAT 2006). This is the primary spawning ground for yellowfin tuna but other spawning grounds have been identified in the GOM and the SE Caribbean Sea. This largely accounts for the concentration of movement vectors to these areas (Prince and Goodyear, this volume, their Figure 3).

The tag-recapture patterns of yellowfin tuna around Bermuda can provide estimates of residence time around the Bermuda Seamount and possible movement patterns (Luckhurst et al. 2001). The 3 recaptures outside Bermuda waters (2 off Puerto Rico, one off Cape Hatteras) demonstrate regional demographic connectivity between Bermuda and other areas of the NW Atlantic. These move-

ment vectors confirm the need for regional and international management regimes for such a highly migratory species as yellowfin tuna.

Atlantic patterns of movement in yellowfin tuna are similar to those noted in the Pacific. For example, acoustic tagging of large, adult yellowfin off Hawaii (Brill et al. 1999) evaluated both vertical and horizontal movements. These fish spent 60–80% of their time in the surface layer (< 100 m) and maximum depth appeared to be limited by water temperatures 8° C colder than the surface layer. Horizontal movements were restricted to within 18.5 km of the coast and fish were often associated with floating objects. Acoustical tracking of yellowfin tuna off California (Block et al. 1997) indicated that the fish spent the majority of their time above the thermocline and only made short, periodic dives to deeper, colder water. However, as these fish were only tracked for 2–3 d. it was not possible to make a meaningful assessment of horizontal movements. Klimley et al. (2003) monitored the presence of yellowfin around a seamount in the Gulf of California using acoustical tags and found that 6 of 23 tagged fish were present for periods of 2–6 weeks. Five other tagged fish were seasonally resident at the seamount or were detected regularly for periods of 6–18 months.

Wahoo

Wahoo is one of the most important commercial species in the wider Caribbean but it has attained increased recreational significance throughout the NW Atlantic in recent years. Little is known about wahoo movement patterns in the western North Atlantic but adult wahoo appear to engage in long distance, seasonal movements (Oxenford et al. 2003) apparently extending into cooler waters in the summer months. They almost certainly move across the Exclusive Economic Zones of a number of countries in the Caribbean region.

There are virtually no data with regard to wahoo tag-recaptures in the NW Atlantic. A tagging program in the SE Caribbean (250 tagged fish) produced no recaptures whereas there was one recapture out of 15 tagged fish in Bermuda. However, it is unknown if this tagged wahoo remained in Bermuda waters during its time at liberty (10 months) or moved away and then returned to Bermuda on a seasonal migratory route (Luckhurst et al. 2001). With such limited data, it is not possible to resolve whether this fish was a Bermuda resident or was on an annual migration past Bermuda. It is probable that wahoo found in Bermuda waters are a combination of a resident population with annual pulses of migrating fish using the Bermuda seamount as a feeding station. The strong seasonality of landings of wahoo in Bermuda with peaks in Spring and Fall

(Luckhurst and Trott 2000) tends to support the concept of an annual seasonal migration past Bermuda (Luckhurst et al. 2001).

Recent PSAT tagging results of wahoo confirm that wahoo move considerable distances e.g., 580 km in 54 d (Thiesen and Baldwin In press). The movement patterns of 3 tagged fish were largely north-south and movement tracks appeared to be related to the position of the Gulf Stream. The data also indicated that wahoo spent most of their time in relatively shallow water but made dives to about 200 m. With this limited data set it is not possible to generalize, but preliminary results suggest that wahoo do not dive to the depths observed in blue marlin and swordfish. This in turn may indicate that they have a narrower preferred thermal range than the other species. Thiesen and Baldwin (In press) stated that their fish remained in a narrow 5° C temperature range (20–25° C).

It is thought that further technological developments (including miniaturization) in electronic tags will greatly increase our ability to determine movement patterns of large pelagic species and that the data can be used to better define habitat use in the pelagic environment. This information can be used to enhance our understanding of fishery exploitation patterns and can assist in the formulation of improved management regimes in pelagic fisheries.

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Strategic Investments in Large Pelagic Research

Nancy B. Thompson

National Oceanic and Atmospheric Administration

Eric D. Prince

National Oceanic and Atmospheric Administration

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STRATEGIC INVESTMENTS IN LARGE PELAGIC RESEARCH

Nancy B. Thompson and Eric D. Prince

*NOAA Fisheries, Southeast Fisheries Science Center, 75 Virginia Beach Drive, Miami, Florida
33149 USA*

The Southeast Fisheries Science Center (SEFSC) of the US NOAA Fisheries provides much of the US science advice for the management of Highly Migratory Species (HMS) in the Atlantic, Gulf of Mexico and US Caribbean Sea. These stocks include the tunas, sharks, billfishes and swordfish all of which are targeted either commercially or recreationally or both in US waters. These species are managed internationally through membership to the International Commission for the Conservation of Atlantic Tunas (ICCAT); however, while the US is an ICCAT member, few Caribbean nations are members. According to ICCAT (2006), both blue and white marlin are overfished and undergoing overfishing; western Atlantic sailfish are undergoing overfishing and fully exploited; western Atlantic Bluefin tuna are overfished and undergoing overfishing; north Atlantic swordfish are no longer undergoing overfishing and are rebuilding; and Atlantic yellowfin tuna are neither undergoing overfishing nor are overfished.

The commercial ex-vessel value and recreational value continue to provide sufficient incentive for exploitation. For example, the ex-vessel value for tuna and swordfish steaks in 2003 and 2004 was US\$22,000,000 and US\$16,000,000, respectively. In Puerto Rico, the estimated value of recreational billfish fishing in 1994 was estimated at US\$44,000,000 per year. A 1999 study (Sutton et al. 1999) estimated that for the US Gulf of Mexico, the charter boat industry produced 1000 jobs and total economic output of US\$45,000,000 per year. This study also identified HMS as the most sought after species by the Gulf of Mexico charter boat industry. The billfishes are highly prized recreational targets globally, yet there is a lack of understanding of much of their life history. In 2000, the SEFSC first developed an "Atlantic Billfish Research Plan" currently in version 4 and revised in 2004. The objective of the plan was to provide guidance on research priorities to reduce uncertainty in ongoing stock assessments to improve the biological basis for management and rebuild the stocks. This plan prioritized information needs as: biology and ecology, including age and growth, fecundity, species identification and stock structure; analytical methodology and tool development and implementation; and fishery research including gear solutions to minimizing bycatch. As a result of this plan, increasing investments in funding of applied research began in 2002 and with an increasing number of research partners and collaborators. One measure of increasing the

body of knowledge on which to base management is the number of publications resulting from these increases in investment. From 2004 to 2006, the number of publications specific to billfish life history, ecology, and potential impacts from fishing increased from less than 5 to 8 in 2005 and to 23 in 2006. Continued investments into research organized around a working hypothesis will progress towards improving the science advice and basis for management world wide.

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Eric D. Prince

National Marine Fisheries Service

C. Phillip Goodyear

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CONSEQUENCES OF OCEAN SCALE HYPOXIA CONSTRAINED HABITAT FOR TROPICAL PELAGIC FISHES

Eric D. Prince¹ and C. Phillip Goodyear²

¹National Marine Fisheries Service, Southeast Fisheries Science Center, 75 Virginia Beach Drive, Miami, Florida 33149 USA, E-mail eric.prince@noaa.gov

²1214 North Lakeshore Drive, Niceville, Florida 32578 USA

ABSTRACT Large areas of cold hypoxic water occur as distinct strata in the eastern tropical Pacific and Atlantic oceans as a result of high productivity initiated by intense nutrient upwelling. Recent studies show that this stratum restricts the depth distribution of tropical pelagic marlins, sailfish, and tunas in the eastern tropical Pacific by compressing the acceptable physical habitat into a narrow surface layer. This layer extends downward to a variable boundary defined by a shallow thermocline, often at 25 m, above a barrier of cold hypoxic water. The depth distributions of marlin and sailfish monitored with electronic tags and mean dissolved oxygen (DO) and temperature profiles show that this cold hypoxic environment constitutes a lower habitat boundary in the eastern tropical Pacific, but not in the western North Atlantic, where DO is not limiting. However, hypoxia-based habitat compression has not actually been demonstrated in the eastern tropical Atlantic Ocean, despite this region having similar oceanographic features to the eastern tropical Pacific. This paper explores the possibility that habitat compression of tropical pelagic fishes exists in the eastern tropical Atlantic and examines possible consequences of this phenomenon. We used Atlantic-wide catches of yellowfin tuna (*Thunnus albacares*) as an example why habitat compression off west Africa could eventually affect the total Atlantic stock.

RESUMEN Extensas áreas con aguas relativamente frías y bajo contenido de oxígeno (hipoxia) pueden ocurrir en el Pacífico y Atlántico Tropical oriental como resultado de alta productividad biológica en zona de upwelling. Estudios recientes demuestran que estos estratos restringen la distribución vertical de especies pelágicas tropicales como los marlines, pez vela y atunes en el Pacífico tropical oriental al comprimir el hábitat de estas especies a una termoclina poco profunda, a menudo solo 25 m, sobre una barrera de agua fría y con bajo contenido de oxígeno. Las distribuciones vertical de marlines y pez vela monitoreadas con marcas electrónicas y perfiles de oxígeno disuelto (OD) y temperatura muestran que este ambiente relativamente frío y bajo contenido de oxígeno constituye una barrera del hábitat en el Pacífico tropical oriental, pero no el Atlántico Norte occidental donde el OD no es limitante. La compresión del hábitat basada en la hipoxia no se pudo demostrar en el Atlántico tropical oriental, a pesar de que esta región tiene características oceanográficas similares a las del Pacífico tropical oriental. Este documento explora la posibilidad de la existencia de hábitats comprimidos para especies de peces tropicales y examina las posibles consecuencias de este fenómeno. Utilizamos colectas de albacore (*Thunnus albacores*) como ejemplo del efecto de la compresión del hábitat en la parte oeste de África y su efecto en el stock del Atlántico.

Large areas of cold, oxygen-depleted (hypoxic) waters are permanent features of the eastern tropical Pacific and Atlantic oceans (Helly and Levin 2004), a result of intense nutrient upwelling (Cushing 1969, Diaz 2001). Here we use electronic tags (Siebert and Nielson 2001) to show that these cold, hypoxic strata compress the acceptable physical habitat of marlin and sailfish into a shallow surface layer, with important ecological and fisheries consequences.

Very little data exist to characterize the habitat depths of tropical pelagic billfishes and tunas, even though these features are critical for monitoring population abundance. We investigated habitat depth of marlin and sailfish using pop-up satellite archival tags (PSAT, Siebert and Nielson 2001). We monitored 19 billfish an aggregate of 801 d in western North Atlantic habitats where dissolved oxygen (DO) concentrations are not limiting, and 13 billfish an aggregate of 429 d in the eastern tropical Pacific, where hypoxic conditions are often as shallow as 25 m (Figure 1A). We stratified the amount of time spent by each fish, and its deepest dive dur-

ing successive 6 hr periods into strata of ≤ 50 m, > 50 m, > 100 and > 200 m. Pacific billfish remained within the shallowest strata, while Atlantic billfish were much more likely to venture deeper (Figure 1B, a & b). Our analyses showed markedly different vertical habitat use (highly significant $P < 0.001$) in the two studies areas.

The spatial extents of acceptable habitats for some estuarine and shallow demersal reef fishes are known to respond to variation in DO (Eby and Crowder 2001, Stanley and Wilson 2004). Our findings show this phenomenon also exists at a much larger scale for pelagic fishes in the tropical oceans. In our Pacific study area, DO levels (Fonteneau 1997, Prince and Goodyear 2006) of

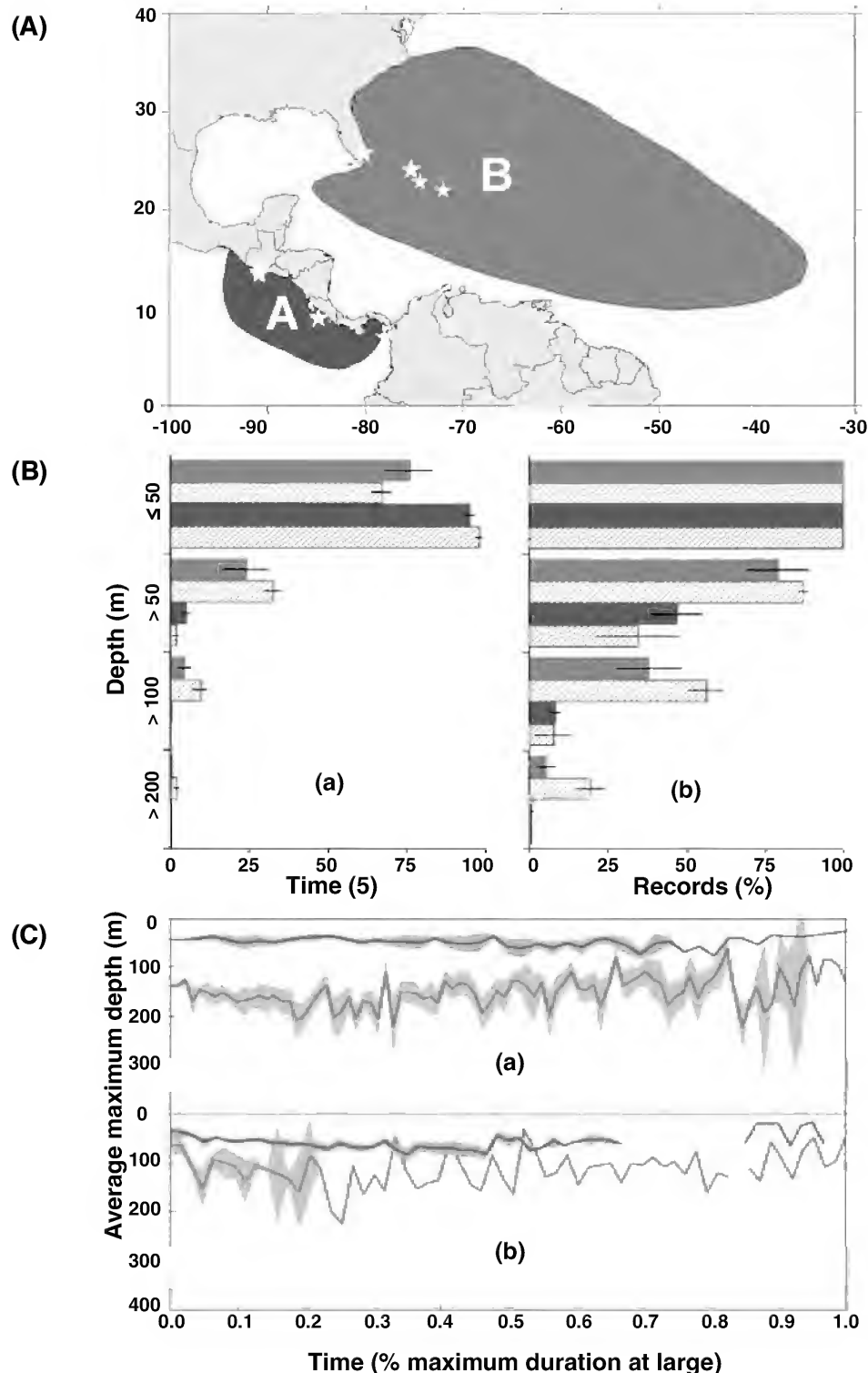


Figure 1. (A) Pacific (A) and Atlantic (B) basin study areas as defined by the displacements of electronic tags deployed on billfish from point of release (stars) to where the tags transmitted data to the Argos satellite system. (B) Proportion of time at depth (a) and proportion of records with dives to depth (b). Atlantic and Pacific billfish are denoted by red and blue, respectively. Solid bars represent sailfish and crosshatched bars denote marlins. Error bars are one standard error. (C) Maximum observed depths of marlin (a) and sailfish (b) during successive 6-hr intervals after release (Prince and Goodyear 2006). Pacific observations are above the Atlantic observations, respectively, and shaded areas denote variability (\pm one standard error). Solid lines represent the 6-hour average maximum depths visited by each species. Reprinted with permission from the *Journal of Fisheries Oceanography* 15(6):451–464, 2006.

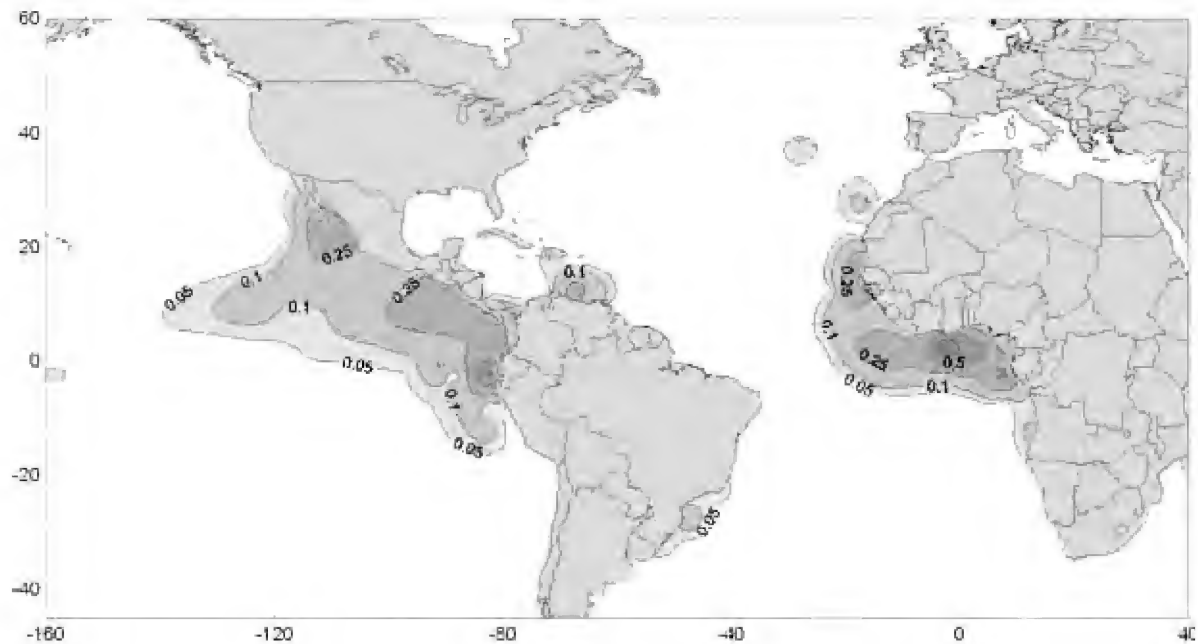


Figure 2. Distribution of skipjack tuna and yellowfin tuna catch estimates in the Atlantic and eastern Pacific Oceans from FAO data, 1955–2000. Catches were normalized to the maximum average catch per 5° cell. Reprinted with permission from Fisheries Oceanography 15(6):451–464, 2006.

1.5 ml/l occur at about 75 m and this depth appears to form the lower threshold of habitat use for our Pacific billfish (Figure 1C, a & b). Conversely, DO levels rarely fell below 3.5 ml/l (Fonteneau 1997, Prince and Goodyear 2006) and did not appear to constrain vertical habitat use of our Atlantic marlin or sailfish (Figure 1C). The extremely shallow depth of acceptable habitat in the Pacific study area arising from nutrient upwelling in the region also restricts this highly productive environment to the very near surface. We feel that this habitat compression facilitates closer physical proximity of predator and prey in the same habitat, which would provide enhanced foraging opportunities that may contribute to faster growth and larger mean sizes of apex predators (Beardsely 1980, Prince and Goodyear 2006).

We have discovered strong quantitative evidence that the depth of the acceptable habitat for billfish is shallower in our eastern Pacific study area than the western North Atlantic. We contend that this difference is a consequence of the cold hypoxic water underlying the shallow thermocline in the eastern Pacific, not present in the western North Atlantic. The same environmental features that limit acceptable habitat to a very shallow surface layer also make the fishes more vulnerable to exploitation, as evidenced by high catches of tropical pelagic skipjack and yellowfin tunas in these areas (Figure 2). Where the habitat is compressed into a shallow surface layer, fish are fully exposed to highly efficient surface gears such as purse

seines, a combination that can threaten resource productivity and sustainability. This vulnerability is particularly important for bycatch species like blue marlin that have lower tolerances to fishing mortality than the target species, e.g., yellowfin tuna (Goodyear 2005).

Although the eastern Atlantic has many of the same oceanographic features of the eastern tropical Pacific (Fonteneau 1997, Prince and Goodyear 2006), Atlantic habitat compression of tropical pelagic fishes has yet to be documented with empirical data (Prince and Goodyear 2006). If hypoxia-based habitat compression does exist in the eastern Atlantic, the question becomes: Is this an issue of concern in the western north Atlantic? The International Commission for the Conservation of Atlantic Tunas (ICCAT) manages yellowfin tuna as a total Atlantic stock and this stock structure hypothesis is confirmed, in part, by conventional tagging results that demonstrate connectivity on both sides of the Atlantic (Figure 3). As many of these species are already fully exploited or overfished, increased vulnerability of yellowfin tuna in compressed habitat off West Africa could eventually affect the entire Atlantic stock.

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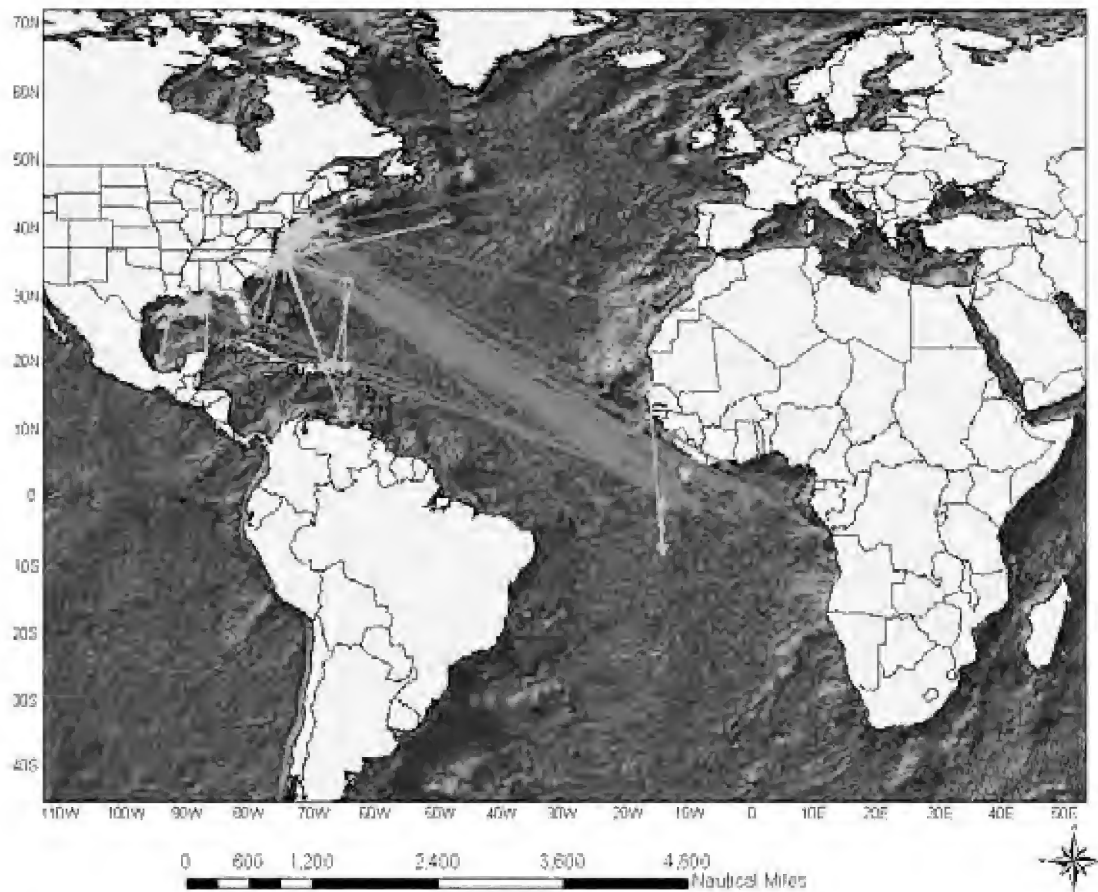


Figure 3. Conventional tag recoveries for yellowfin from the Southeast Fisheries Science Center's Cooperative Tagging Center, Miami, FL., 1954–2005. Red displacements illustrate transatlantic movements and yellow displacements show western or eastern Atlantic movements. Arrows indicated direction of movement.

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Freddy Arocha

Universidad de Oriente, Venezuela

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SWORDFISH REPRODUCTION IN THE ATLANTIC OCEAN: AN OVERVIEW

Freddy Arocha

Instituto Oceanográfico de Venezuela, Universidad de Oriente, Apartado de Correos No. 204, Cumaná-6101, VENEZUELA, E-mail farocha@sucre.udo.edu.ve; farochap@gmail.com

ABSTRACT There are 3 unit stocks of Atlantic swordfish, *Xiphias gladius*, separated into Mediterranean, North and South Atlantic with no precise delimitation between them, and each contains its spawning grounds far from stock boundary areas. This overview characterizes the reproductive information for each stock unit and describes reproductive metrics in detail. Spawning in the western North Atlantic consists of 2 spawning groups: one in open ocean waters and the other in waters close to land masses and fast current systems. Spawning occurs from December to June within the subtropical area (13°N–35°N). Within the Mediterranean, spawning takes place between June and August, and appears to be restricted between 35°N and 40°N. The information for the South Atlantic is limited, but spawning concentrations are present in April–June on the western side off Brazil and the equatorial area, and from October to March in the central-eastern equatorial area. In the western North Atlantic, females are observed to mature at larger sizes ($M_{f50} = 178.7$ cm) and older ages (age 5.03) than in the South Atlantic ($M_{f50} = 156$ cm) and Mediterranean Sea ($M_{f50} = 142.2$ cm). Estimates of batch fecundities in swordfish in the Atlantic Ocean appear to be similar, and can reach up to 8–9.9 million eggs per spawn.

RESUMEN En el Océano Atlántico existen 3 unidades de stock de pez espada, *Xiphias gladius*, conformadas por la del Mediterráneo, la del Atlántico Norte y la del Atlántico Sur, no contentan con una delimitación precisa entre ellas, y cada una contiene sus áreas de reproducción y desove alejadas de las zonas límites de las unidades de stock. Esta visión general caracteriza la información reproductiva en cada unidad de stock y describe la reproducción en detalle. La reproducción del pez espada en el Atlántico nor-occidental está compuesta por dos grupos reproductivos: uno en aguas oceánicas y otro en aguas cercanas a las costas y de fuertes corrientes. La reproducción ocurre de diciembre a junio en el área subtropical (13°N–35°N). En el Mediterráneo, la reproducción ocurre entre junio y agosto, donde parece estar restringida entre los 35°N y 40°N. La información para el Atlántico Sur es limitada, pero concentraciones para la reproducción están presentes de abril a junio en el lado occidental cercano al Brasil y en el área ecuatorial, y de octubre a marzo en el área ecuatorial centro-oriental. En el Atlántico nor-occidental, las hembras maduran a tallas mayores ($M_{f50} = 178.7$ cm) y a edades mayores (edad 5.03) que en el Atlántico Sur ($M_{f50} = 156$ cm) y el Mar Mediterráneo ($M_{f50} = 142.2$ cm). Los estimados de fecundidad por tanda en el pez espada del Océano Atlántico parecen ser similares, y pueden alcanzar hasta 8.0–9.9 millones de huevos en cada desove.

INTRODUCTION

Swordfish (*Xiphias gladius*) are highly migratory meso-pelagic fishes widely distributed throughout tropical and temperate waters between 45°N and 45°S, and in large enclosed basins such as the Gulf of Mexico (GOM), the Caribbean Sea, and Mediterranean seas (Palko et al. 1981, Nakamura 1985). The Atlantic population structure has at least three genetically distinct units: Mediterranean, western North Atlantic, and South Atlantic (Kotulas et al. 1995, Chow et al. 1997, Alvarado-Bremer et al. 2005). For fishery management purposes, the International Commission for the Conservation of Atlantic Tunas (ICCAT) recognizes a North and South Atlantic stocks separated by an imaginary boundary located at 5°N and a Mediterranean stock separated by the Strait of Gibraltar (ICCAT 2006). Although, the possibility for a northeast Atlantic unit is not excluded, the admixture with Mediterranean swordfish may confound analyses (Chow and Takeyama 2000, Kotulas et al. 2006).

The information on swordfish reproduction in the Atlantic is fragmented and limited. The temporal and spatial spawning patterns have been inferred from the abundance of larvae (Sella 1911, Tåning 1955, Gorbunova 1969, Grall et al. 1983, Govoni et al. 2000), gonad assessment by means of a gonad index (de la Serna et al. 1992, Arocha and Lee 1995, Mejuto and García 1997), and by microscopic examination of developmental stages of oocytes (Taylor and Murphy 1992, Arocha 1997, Correiro et al. 2004). Most authors have inferred swordfish spawning patterns in the Atlantic Ocean using a single method, although some studies have attempted to integrate several methods with more than one technique (Arocha 1997, Govoni et al. 2003, Correiro et al. 2004).

In recent years there has been an increasing need for reproductive population parameters in marine fishes, which are essential to obtain accurate estimates of the effect of fishing on the reproductive potential of the stock (Mace 1993, Murawski et al. 2001). Size-and-age-at-maturity and specific fecundity are basic parameters to estimate

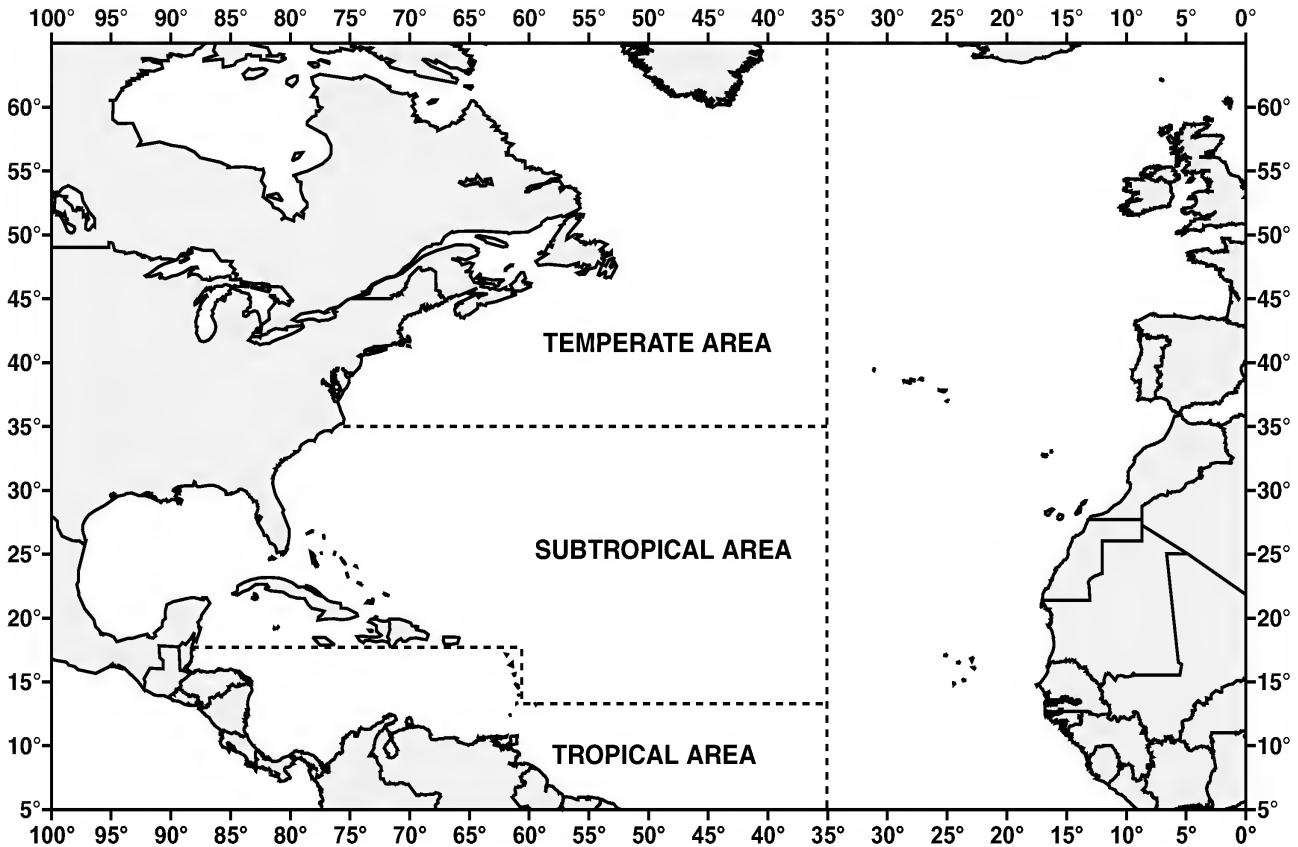


Figure 1. Map of the North Atlantic Ocean showing the boundaries of the 3 areas (i.e., temperate, subtropical, tropical) into which the study on swordfish reproduction in the western North Atlantic was divided (Arocha 1997).

spawning potential ratio (SPR) in fishery stock assessments (Goodyear 1993) and spawner-recruit relationships. Swordfish reproductive population parameters have been estimated for the three recognized stock units in the Atlantic (de la Serna et al. 1996, Arocha 1997, Hazin et al. 2001), but assumptions and techniques differ between studies.

The present paper is an overview of the temporal and spatial spawning patterns currently known for swordfish throughout its Atlantic Ocean distribution. Reproductive population parameters (maturity-at-size and batch fecundity) will be reviewed and contrasted by stock structure. This paper provides an integrated view of the spawning of swordfish in the Atlantic Ocean as is currently known.

MATERIALS AND METHODS

Selection of data

The data selected for the description of temporal and spatial spawning patterns were obtained from the most recent and comprehensive studies available for the Atlantic Ocean, these include: Arocha (1997) and Govoni et al. (2003) for the western North Atlantic; Mejuto and García

(1997), and Ueyanagui et al. (1970) for the South Atlantic; Cavallaro et al. (1991), de la Serna et al. (1996), Tserpes et al. (2001), Correiro et al. (2004), and Macias et al. (2005) for the Mediterranean Sea.

The data selected for the review on reproductive population parameters come from the studies of de la Serna et al. (1996) for the Mediterranean stock, Arocha (1997) for the North Atlantic stock, and Hazin et al. (2001, 2002) for the South Atlantic stock.

Data for spawning indication and location

North Atlantic stock. The region was divided into the 3 areas used in the study of Arocha (1997) for the western North Atlantic. The areas were defined as: tropical (5°–13°N in the Atlantic side and 5°–18°N in the Caribbean side), subtropical (13°–35°N in the Atlantic side and 18°–35°N in the Caribbean side), and temperate (35°–55°N) (Figure 1). The subtropical area was further subdivided into the Atlantic subarea (ATL) which included specimens caught in the Atlantic Ocean outside the Antillean Island chain; the GOM and Windward Passage subarea (GOMWP) which included specimens caught in the

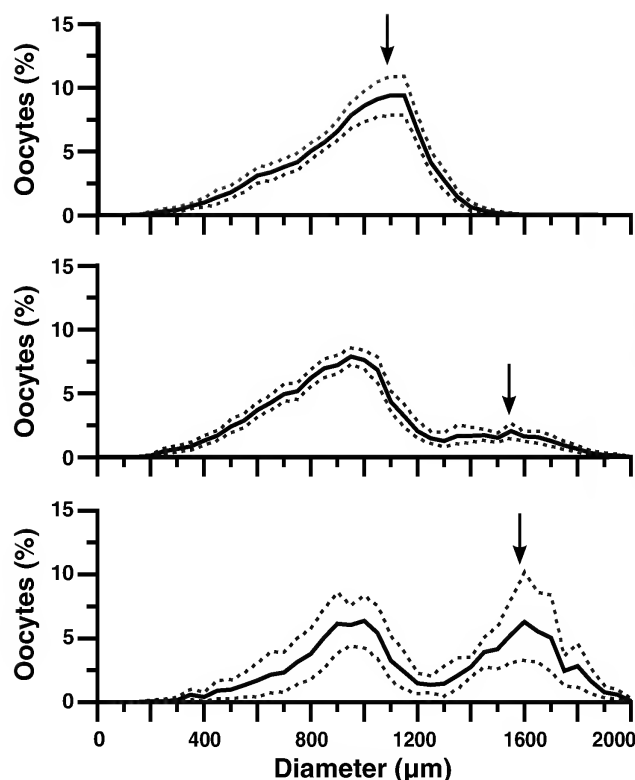


Figure 2. Typified size frequency distributions of fresh whole oocytes in spawning females in the western North Atlantic (after Arocha 2002). a) Bootstrapped frequency distribution of migratory nucleus oocytes (arrow) as the most advanced group of oocytes; b) Bootstrapped frequency distribution of oocytes with unovulated hydrated oocytes (arrow) as the most advanced group of oocytes; c) Bootstrapped frequency distribution of oocytes with ovulated hydrated oocytes (arrow) as the most advanced group of oocytes, dashed lines depict 95% confidence limits; d) Image of whole hydrated (hy) and migratory nucleus (mn) oocytes.

Windward Passage, Yucatan Channel, and the GOM; the Straits of Florida and southeastern US subarea (SOFSE) which included specimens east of 82°W in the Straits of Florida to 35°N, along the southeastern US coast.

Spawning was inferred from a combination of techniques. Classification of sexually mature females (>150 cm lower jaw-fork length, LJFL) in spawning condition was based on the relative gonad index (RGI) (Erickson et al. 1985). This index was adjusted to the mean oocyte diameter of 10 of the largest and most advanced group of oocytes (MAGO) in the ovary such that the RGI value would ensure that females were at an advanced maturity stage (Arocha 1997). The resulting RGI value of the RGI vs mean MAGO diameter was estimated by an iterative search method to obtain the best fit of 2 straight lines (Somerton 1978, Cayré and Laloë 1986, Arocha 1997). The point of intercept of the 2 lines would be the RGI value at which oocytes would be considered to complete vitellogenesis. The estimated RGI value (27.64), termed *spawn* RGI, was utilized to indicate that spawning was about to happen or occurring. Spawning females were defined as those presumed to spawn within 24–48 h based on the

presence of migratory-nucleus phase or hydrated oocytes as the most advanced stage of development in the gonad or those that had spawned in the last 12–24 h and contained post-ovulatory follicles (POF) in the gonad of recently spawned females. Spawning females were identified using typified size frequency distributions of fresh oocyte diameters (Figure 2) as defined by Arocha (2002). Once spawning females were defined and identified, the combined information of the seasonal distribution of spawning females, the seasonal distribution of young larvae (<10 days from fertilization [DFF], from Govoni et al. 2003), and the seasonal distribution of females with mean maximum RGI (maxRGI, RGI > 27.64) were used to describe the seasonal shift in time and location of imminent spawning in the western North Atlantic.

South Atlantic Stock. The classification of sexually mature females in spawning condition was based on the gonad index traditionally used by European scientists working on swordfish (e.g., Kume and Joseph 1969), combined with examination and measurement of oocytes in histological sections from the studies of Hazin et al. (2001, 2002). The temporal and spatial distribution of spawning

TABLE 1

Monthly mean oocyte diameter of the most advanced group of oocytes ($MAGO$), standard error (SE), oocyte diameter range (μm), and sample size of fish (n) of sexually active female swordfish ($MAGO > 1000 \mu m$) in the western North Atlantic.

	$MAGO$	SE	range (μm)	n
January	1423	46.8	1108–1818	27
February	1336	30.8	1048–1825	48
March	1289	99.0	1012–1777	8
April	1487	121.6	1060–1888	8
May	1633	64.8	1142–2078	19
June	1305	121.9	1080–1611	4
July	—	—	—	—
August	1110	47.9	1062–1158	2
September	1145	—	—	1
October	1097	—	—	1
November	—	—	—	—
December	1363	56.2	1096–1709	12

swordfish in the South Atlantic was inferred from gonad indices (GI) estimated from female fish caught by Spanish longline vessels during 1986–1996 (Majuto and Garcia 1997). The authors considered that female fish with a GI > 3.0 'to be spawning or with ripe egg', and calculated GI values for 2 size groups of fish, small (<165 cm L_TL) and large (>165 cm L_TL). Additionally, an overall mean GI value and an overall mean GI maximum (GI_{max}) value for each size group were then calculated and grouped into

spatial areas of 5X5 degree squares. However, in the absence of detailed gonad measurement data for the South Atlantic and with the knowledge that length based GI values (e.g., Korne and Joseph 1969) for near spawning fish are > 5.0 (Aricha and Lee 1993, Corriero et al., 2004), only data from the large fish group (>165 cm L_TL) and overall mean GI maximum (GI_{max}) value grouped into 5X5 degree squares were used to describe seasonal and spatial changes in the present work.

Mediterranean stock. The classification of sexually mature females in spawning condition was based on the length based gonad index (GI) of Korne and Joseph (1969), combined with examination and measurement of sectioned oocytes in histological slides of interovarian inclusions from the studies of Corriero et al. (2004) and Macías et al. (2005). The time and location of imminent spawning was inferred from the combination of females with maximum gonad indices, the presence of hydrated oocytes in their ovaries, and the seasonal distribution of eggs and young larvae (age = 5 d, from Cavallaro et al. 1991).

Data for reproductive population parameters

North Atlantic Stock. Estimates for the maturity fraction included only specimens caught during the spawning period. For the age maturity fraction, direct age was determined from otolith cross sections (Richardt et al. 1996). Estimates of hatch fecundity were estimated as the number of fresh unovulated and fully hydrated whole oocytes (Figure 2b) from the mean of three ash samples taken from both ovaries and related to the ovary tissue weight. In the

TABLE 2

Monthly relative gonad index of female swordfish (>150 cm lower-jaw-fork-length) in the 3 areas of the western North Atlantic, with mean relative gonad index ($RG\bar{I}$), standard error (SE), and sample size of fish (n).

	Temperate area			Subtropical area			Tropical area		
	$RG\bar{I}$	SE	n	$RG\bar{I}$	SE	n	$RG\bar{I}$	SE	n
January	7.3	0.64	8	29.2	4.18	96	6.9	0.58	5
February	6.9	0.28	19	41.0	3.36	114	7.1	0.57	47
March	6.7	0.63	9	21.9	4.70	44	7.8	0.80	13
April	6.3	0.29	26	18.2	4.79	29	—	—	—
May	6.2	0.63	113	38.2	7.72	26	5.2	0.90	39
June	5.9	0.19	128	30.7	9.89	19	9.4	1.51	15
July	6.4	0.15	269	4.3	—	1	5.8	0.88	12
August	6.7	0.42	86	37.5	12.83	15	5.8	0.77	8
September	5.3	0.17	117	25.6	12.14	10	7.3	0.97	16
October	5.8	0.38	41	24.8	8.56	12	10.1	2.46	15
November	5.8	0.45	16	7.9	0.70	49	25.0	10.74	11
December	—	—	—	21.3	4.32	32	10.4	1.96	40

fish length relationship, a re-scaling factor was used to set the origin at 150 cm LJFL, as no mature individuals were found below that size. F_0 in the model used in Arocha (1997) was defined as the minimum initial fecundity that is present when the fish starts hydrating oocytes. Age was determined directly from anal fin rays sections.

South Atlantic stock. Estimates for the maturity fraction included specimens caught throughout the year. Estimates of batch fecundity were estimated from counts of fixed whole oocytes $>800\ \mu\text{m}$ (from Hazin et al. 2001).

Mediterranean stock. Estimates for the maturity fraction included only specimens caught during the spawning period. Estimates of batch fecundity were estimated from counts of fixed whole oocytes $>650\ \mu\text{m}$ (from de la Serna et al. 1996).

RESULTS

Spawning season and location

North Atlantic Stock. The main spawning season was defined from December to June, based on the presence of fish with mean MAGO above migratory nucleus stage of development ($>1200\ \mu\text{m}$) (Table 1). Some mature fish had vitellogenic oocytes in August, indicating a possible late summer spawning. During other times of the year mean MAGO remained below $1000\ \mu\text{m}$.

The mean relative gonad index (RGI) in females did not indicate spawning activity in the temperate area (Table 2). Mean RGI for females remained below spawning threshold (27.64) and showed no significant differences between months (ANOVA $F=1.494$, $df=10$, 822, $P>0.05$). In the tropical area (Table 2), significant differences in mean RGI between months were observed for females (ANOVA $F=3.748$, $df=10$, 210, $P<0.05$). The differences found were caused by the high mean RGI observed in November and December from a couple of females with mean MAGO $<1200\ \mu\text{m}$ (November). These fish were caught near the limits between the tropical and subtropical areas in the Caribbean side, and a single female with hydrated oocytes (December). In general, mean RGI did not reach the spawning threshold indicating the absence of regular spawning activity throughout the year in the temperate and tropical areas.

In the subtropical area (Table 2), the mean RGI surpassed the spawning threshold (27.64) in January, February, May, June, and August. The mean RGI was high in December, peaked in February, returned to high levels in March and April, and peaked again in May and June. There was another peak in August, and mean RGI remained high in September and October. These observations suggest an

almost year round spawning with peak seasons, but in different locations.

The spatial distribution of spawning in the subtropical area was investigated for 3 subareas. In the ATL subareas, mean maxRGI was high during all months when fishing activity was high, except March when only one spawning female fish was caught (Table 3). Spawning females occurred from December to February (Table 4), in the area northeast of the Antillean Island chain between 18° and 25°N (Figure 3). Spawning females were also encountered in April and May, but far east of the Antillean Island chain between 13° and 15°N . Larvae distribution in the vicinity of the area was restricted to the Antillean Island chain where most larvae were 15–35 DFF from January to March. No data were available for the rest of the season due to the few fishing vessels operating in the area from June to November, but observers on board commercial longliners fishing close to the Anegada Passage during the summer have indicated that ovaries from swordfish gave no indication of being mature or spawned (D. Lee, pers. comm., NOAA-NMFS-SEFSC, Miami, FL).

In the GOMWP, the mean maxRGI was variably high from December to May, and again in October (Table 3). In June, when mean maxRGI was at its lowest value, only one spawning female fish was collected. The rest of the months, all female fish had values below the spawning threshold. Spawning females occurred in the Windward Passage and in the Yucatan Channel from December to March (Table 4). No spawning females were found in the GOMWP during the rest of the year. Larvae distribution was mostly associated with the GOM. In the western GOM larvae were present in the spring/summer (most likely between March and June), but were 20–25 DFF. In the north-central GOM, larvae of <10 DFF were present in all seasons, although the largest concentration of larvae was found during the spring/summer period.

The mean maxRGI for the SOFSE area was variably high in May, June, August, and September (Table 3). The rest of the year, mean maxRGI was below the spawning threshold, except in February and April, when only few spawning female fish were collected. Spawning females were encountered in the SOFSE in February and in May–June (Table 4) and the one spawning female collected in February with migratory-nucleus phase oocytes was found in the SOF. The rest of the spawning females were found in the southeastern waters of the US between 25° and 35°N (Figure 4). Larvae of <10 DFF were only found in the waters of the southeast US during the spring/summer and in summer/fall (likely from July–November) period. Although larvae were found throughout the area in all seasons, most were 15–30 DFF.

TABLE 3

Monthly maximum relative gonad index of female swordfish (>150 cm lower jaw-fork length) in the subtropical area of the western North Atlantic, with mean maxRGI ($\overline{\text{maxRGI}}$), standard error ($S_{\bar{x}}$), and sample size of fish (n) of female swordfish in the Atlantic subarea (ATL), the Gulf of Mexico and the Windward Passage subarea (GOMWP), and the Straits of Florida and southeastern US subarea (SOFSE).

	ATL subarea			GOMWP subarea			SOFSE subarea		
	$\overline{\text{maxRGI}}$	$S_{\bar{x}}$	n	$\overline{\text{maxRGI}}$	$S_{\bar{x}}$	n	$\overline{\text{maxRGI}}$	$S_{\bar{x}}$	n
January	95.7	8.05	21	78.4	27.58	2	—	—	—
February	69.6	3.87	45	71.9	9.00	13	40.5	0.02	2
March	30.9	—	1	82.8	8.95	8	—	—	—
April	102.2	—	1	60.8	8.95	4	30.7	—	1
May	89.4	4.65	3	60.4	—	1	80.5	8.22	7
June	—	—	—	32.4	—	1	105.4	18.58	4
July	—	—	—	—	—	—	—	—	—
August	—	—	—	—	—	—	95.2	18.19	5
September	—	—	—	—	—	—	98.1	4.10	2
October	—	—	—	61.3	26.14	3	—	—	—
November	—	—	—	—	—	—	—	—	—
December	73.5	16.20	7	60.4	12.99	5	—	—	—

South Atlantic Stock. The temporal and spatial distribution of mean GI_{max} show female fish spawning year round along the equatorial Atlantic, although, the number of females with GI_{max} was highest in April–June, and in October–December (Figure 4). The number of females with GI_{max} during October–December were only concentrated in the east equatorial Atlantic. In contrast, during April–June fishes with GI_{max} were mostly concentrated from the central towards the western side of the equatorial Atlantic. Another area of fish with GI_{max} at spawning levels was located east of Trinidad and Martin Vaz Islands (~29°20'W–20°30'S) off the Brazilian coast for the same time period (Figure 4). In January–March, female fish with GI_{max} were located around the Rio Grande Rise (~35°W–32°S), around Trinidad and Martin Vaz Islands, and in the western-central equatorial Atlantic (Figure 4). Fish with GI_{max} at spawning levels were also observed in the center of the equatorial Atlantic in July–September (Figure 4).

Larvae collections obtained from Japanese longliners in the 1960s, indicated potential spawning off Fortaleza and Recife (Brazil) and around Trinidad and Martin Vaz Islands in November–April, and in the central Atlantic from May–October. Larvae were collected over warm waters with sea surface temperatures of 26°C (Ueyanagi et al. 1970).

Mediterranean Stock. Swordfish spawning (based on fish with hydrated oocytes, GI >7.0, and the distribution of eggs and larvae) was localized in the western

Mediterranean, east of the Strait of Gibraltar up to the Balears Islands, in the southern Tyrrhenian Sea (off Sicily) and the Strait of Messina, inside the Gulf of Taranto in the Ionian Sea, and in the Levantine Sea (eastern Mediterranean) southeast of the Island of Rhodes–Greece (Figure 5). Imminent spawning takes place between June and August throughout the Mediterranean Sea. In the western Mediterranean, maturing fish (with vitellogenic

TABLE 4

Total number of female fish (n ; >150 cm lower jaw-fork length) and number of spawning females (SF) during the spawning season in the Atlantic subarea (ATL), the Gulf of Mexico and Windward Passage subarea (GOMWP), and the Straits of Florida and southeastern US subarea (SOFSE) of the western North Atlantic.

	ATL		GOMWP		SOFSE	
	n	SF	n	SF	n	SF
December	46	9	12	1	1	—
January	120	32	11	1	1	—
February	74	30	36	5	9	1
March	9	—	33	3	8	—
April	13	4	5	—	29	—
May	42	13	10	—	17	5
June	—	—	1	—	19	3

SWORDFISH REPRODUCTION IN THE ATLANTIC

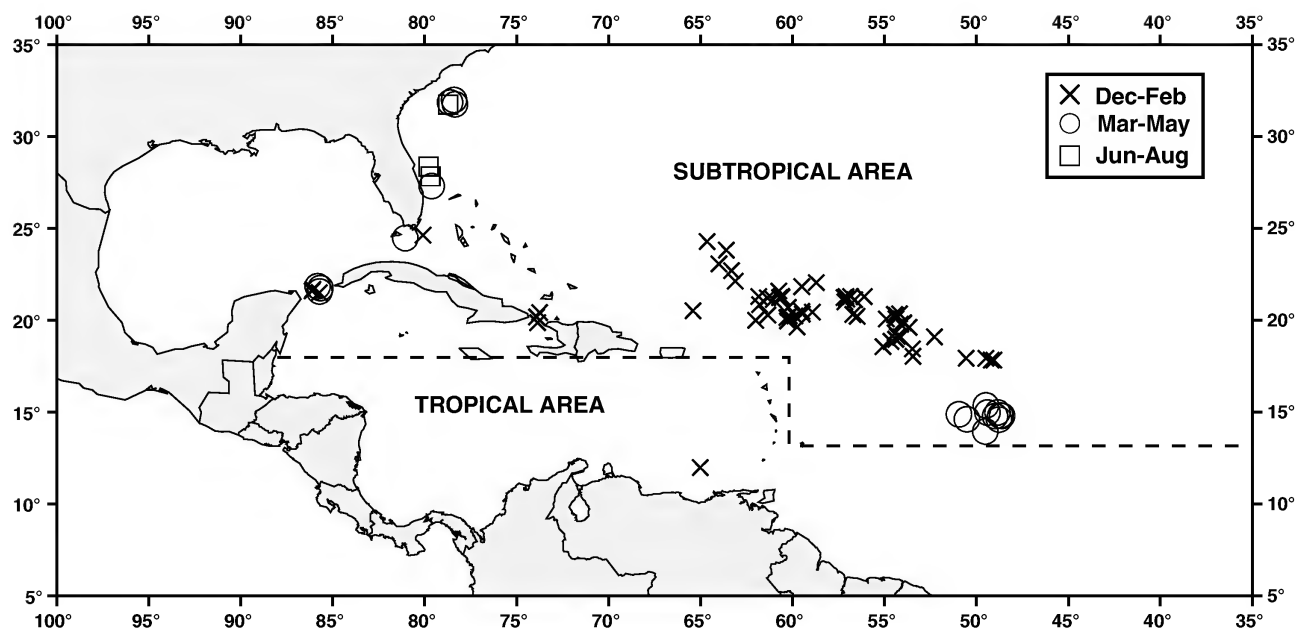


Figure 3. Temporal and spatial distribution of spawning female swordfish by month in the western North Atlantic.

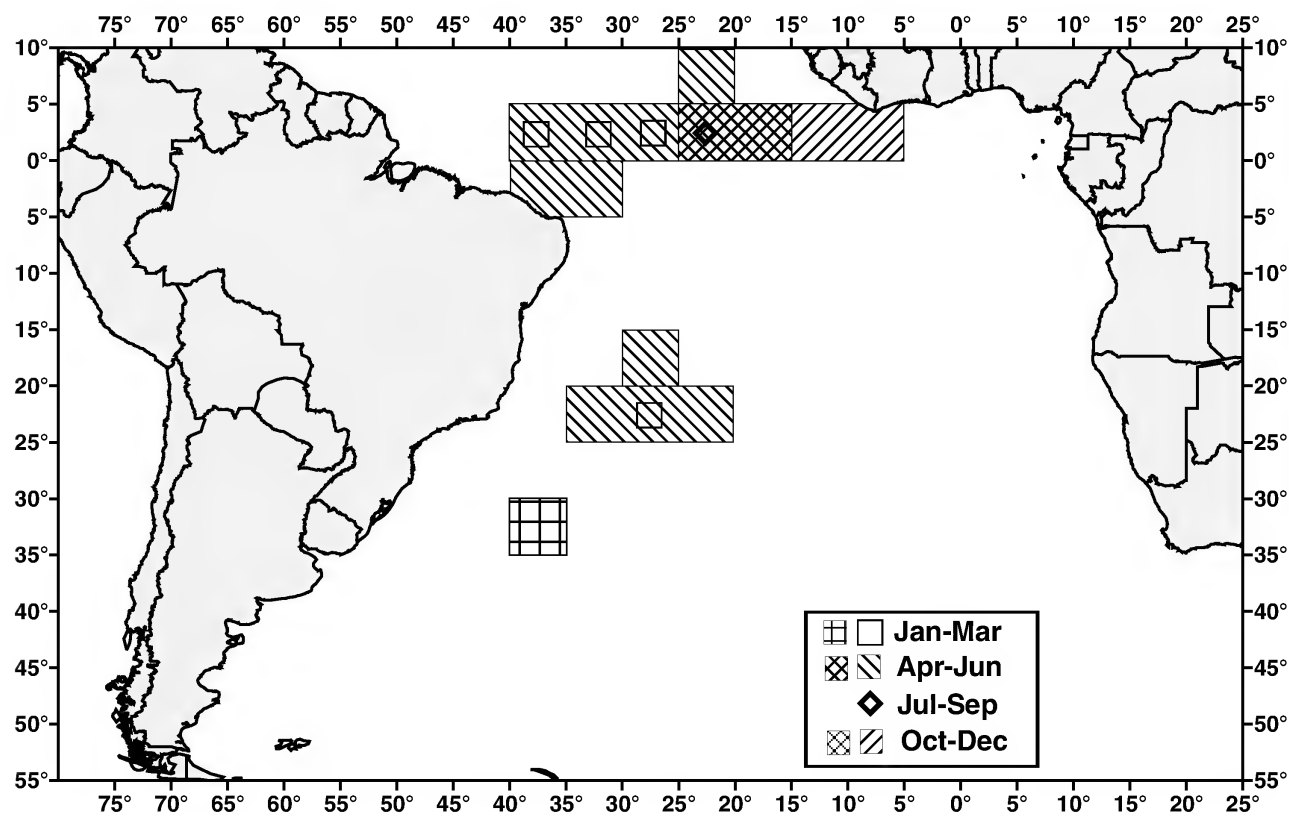


Figure 4. Temporal and spatial distribution of spawning female swordfish by month in the South Atlantic (after Mejuto and García 1997).

oocytes) first appear between April and June, and peak spawning (females with hydrated oocytes and POFs) takes place in July and August. It appears that fish >150 cm LJFL start spawning ($GI > 7.0$) in June, in July all spawning fish are between 120 cm and 230 cm LJFL, and at the end of the season only fish of 130–170 cm LJFL were spawning (Figure 6).

In southern Italy (Tyrrhenian and Ionian Sea, and the Strait of Messina) and around Malta, maturing females (with vitellogenic oocytes) appear between April and early June, and spawning females (with hydrated oocytes and POFs, and $GI > 9.0$) occur from late June through July in the Gulf of Taranto (Ionian Sea), and from July to August in the Strait of Messina and southern Tyrrhenian Sea. Swordfish eggs and larvae were only found in July in the Strait of Messina, the southern Tyrrhenian Sea, and the Ionian Sea. Post-spawning swordfish were located around Malta in July–August. In the eastern Mediterranean, spawning swordfish ($GI > 7.0$) were found only in July, and by August most fish had spawned.

Reproductive population parameters

Maturity fraction. The mean size or age at which 50% of the females are mature (M_{f50}) for each recognized stock were estimated by the various authors using different assumptions and estimation techniques (Table 5). Estimates for maturity fraction of female fish from the North Atlantic stock only included specimens that had been caught during the 6 month (December–June) spawning period when reproductively active females were present. Maximum likelihood estimates of M_{f50} were 178.7 cm LJFL and 5.03 yr old Females attained full maturity at 209.3 cm LJFL and age 8.7. The smallest observed reproductively active female was 150 cm LJFL and age 4. For the South Atlantic stock, estimate of M_{f50} included gonad samples from fish collected off northern Brazil. Swordfish in Brazilian waters mature at an estimated M_{f50} of 156 cm LJFL based on the logistic regression model (Table 5). Females begin to mature at about 125 cm LJFL and attain full maturity by about 195 cm LJFL. In the Mediterranean, least squares estimate of M_{f50} was 142.2 cm LJFL for female fish caught during the three month (June–August) spawning period when reproductively active females were present. They begin to mature at about 110 cm LJFL and attain full maturity at 200 cm LJFL.

Batch Fecundity. In the western North Atlantic, the relation between fish length (LJFL)/age and batch fecundity (B_F) was best explained by a three parameter model that incorporated an additive term to the power model (Table 6). In both batch fecundity relationships (length and age), the minimum initial batch fecundity (F_0) is nearly

the same. Both relationships suggest a steady level of batch fecundity up to the size and age when full maturity is reached (200 cm LJFL / Age 8). After full maturity is attained, batch fecundity increases markedly suggesting that batch fecundity in swordfish is relatively low before females reach full maturity. In the South Atlantic, the relation between fish length (LJFL) and batch fecundity (B_F) was expressed by a linear model (Table 6). For the Mediterranean swordfish, the relation between the fish length (LJFL) and batch fecundity (B_F) of 16 fish was best described by a power function (Table 6).

The mean batch fecundity at length for 29 female swordfish in the western North Atlantic was 3.91×10^6 oocytes (Table 6). These values ranged from 0.99×10^6 hydrated oocytes for a 166 cm LJFL female to 9.00×10^6 hydrated oocytes for a 245 cm LJFL female, thus indicating a wide range in batch fecundity in relation to body size. The mean batch fecundity was 3.84×10^6 oocytes based on age, and it ranged from 2.53×10^6 to 9.00×10^6 oocytes for an age 4 and age 12 female fish. In the South Atlantic, batch fecundity at length for 10 female swordfish ranged from 2.0×10^6 to 8.6×10^6 oocytes for a length range of 160 cm to 194 cm LJFL. Mean batch fecundity was 5.1×10^6 oocytes. For Mediterranean swordfish, mean batch fecundity was 5.90×10^6 oocytes, and it ranged from 2.14×10^6 to 9.91×10^6 oocytes for a length range of 150 cm to 193 cm LJFL.

DISCUSSION

Spawning season and location

Spawning seasonality and location of North Atlantic and Mediterranean swordfish was better defined than for the South Atlantic stock. In the North Atlantic and Mediterranean Sea, spawning was defined and identified by a combination of methods that included ratios that standardize gonad mass to body size, like the GI and RGI (de la Serna et al. 1996, Arocha 1997), microscopic examination and measurement of whole oocytes and oocyte cytology (Arocha 2002, Correiro et al. 2004, Macías et al. 2005), and the distribution of eggs and aged young larvae (Cavallaro et al. 1991, Potoschi et al. 1994, Govoni et al. 2003). Spawning in the western North Atlantic consists of 2 spawning groups proposed by Arocha (1997) and later confirmed by Govoni et al. (2003). The first is in open ocean waters south of the Sargasso Sea and east of the Lesser Antilles, and the second in waters relatively close to land masses and fast current systems like the Windward Passage, Yucatan Channel/Loop Current, Straits of Florida/Gulf Stream. Spawning in open ocean waters begins in December through May, although the data collected in

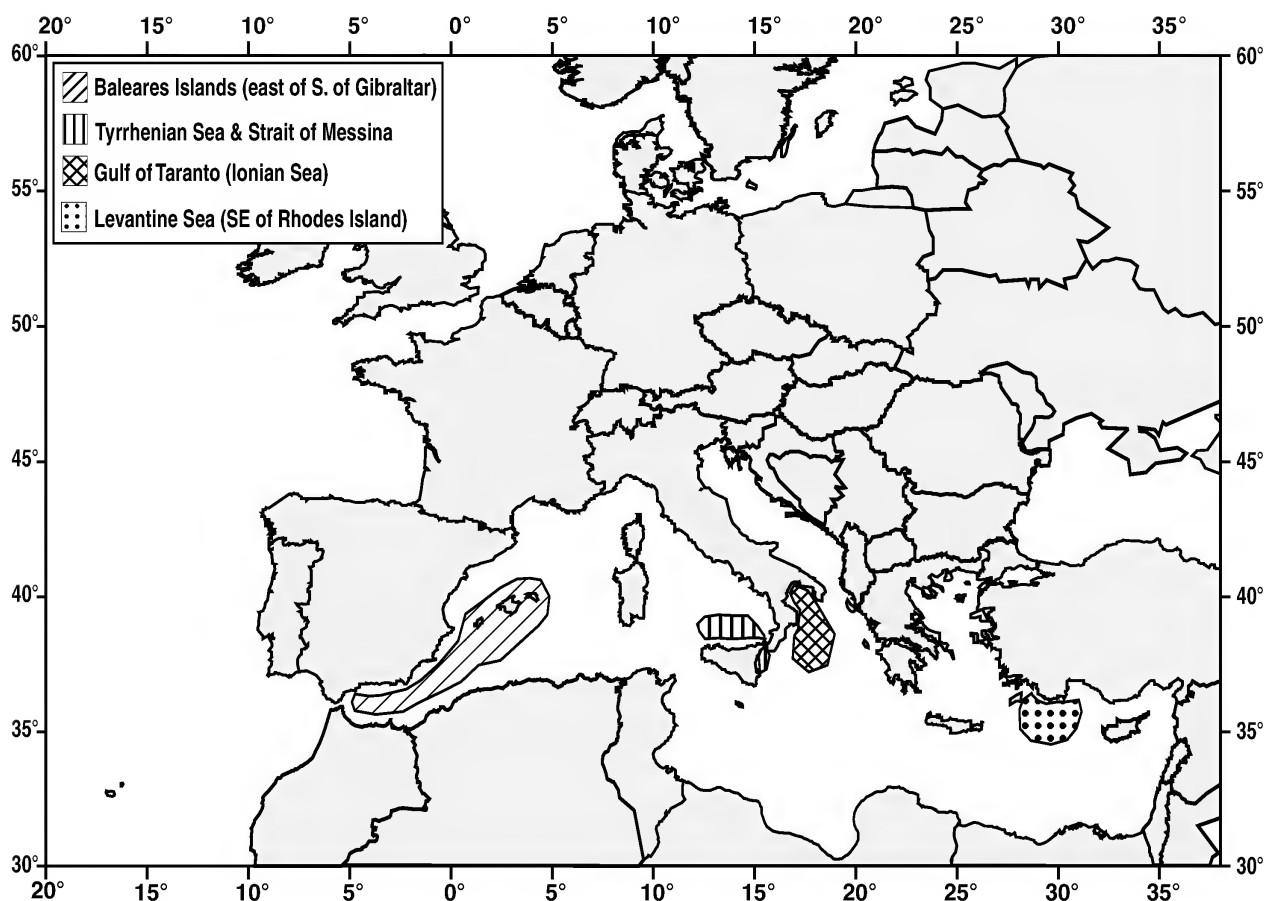


Figure 5. Spatial distribution of spawning female swordfish in the Mediterranean Sea. June–August spawning occurs in the area east of Gibraltar to the Balearic Islands, in the southern Tyrrhenian Sea and the Strait of Messina. Spawning in June–July takes place in the Gulf of Taranto (Ionian Sea), and in the Levantine Sea spawning is in July.

March was low. Larvae (<20 mm) from south of the Sargasso Sea peak from February to April (Tåning 1955) and transit to the Lesser Antilles and into the Caribbean during the first half of the year (Grall et al. 1983, Govoni et al. 2003). The abundance of larvae in the Lesser Antilles (Tibbo and Lauzier 1969, Markle 1974) and the large numbers of juveniles caught by the Venezuelan longline fishery during the second half of the year (Arocha 1997) indicate the southeastern Caribbean as a nursery area. The group spawning close to land masses and strong currents spawn progressively in an east to west and northwest direction as the season progresses. Spawning begins in December through March in the Windward Passage and Yucatan Channel, young larvae from this spawning group concentrate in the GOM during the spring/summer season (Govoni et al. 2003). Additionally, the large number of juveniles discarded by the US longline fishery (Cramer 1996) denote the GOM as a nursery area. Later in the season, the group spawns in the Straits of Florida up to 35°N from May to June, coinciding with spawning dates

and abundances of young larvae in late spring and summer (Govoni et al. 2003). Similarly, juvenile discards from the longline fishery (Cramer 1996) and the larval abundance in the Charleston Bump area (Govoni et al. 2000) also indicate that the waters of the southeastern US serve as a nursery area.

The presence of spawning females in the subtropical area of the western North Atlantic appears to be associated to movements between feeding grounds and spawning grounds. Adult swordfish seem to move between spawning grounds and energy-rich feeding areas of higher latitudes (temperate area) as inferred from the information on selected tagged recaptured specimens obtained from historical data (Brown 1995, Jones et al. 1996). Smaller females and most males which reside at lower latitudes (south of 35°N) show limited movements conditioned by the seasonal displacement in latitude of warm isotherms (24–25°C) (Arocha 1997, Weidner et al. 1999, Weidner et al. 2001), most likely because of their restricted movement ability and reduced capacity to compensate their body

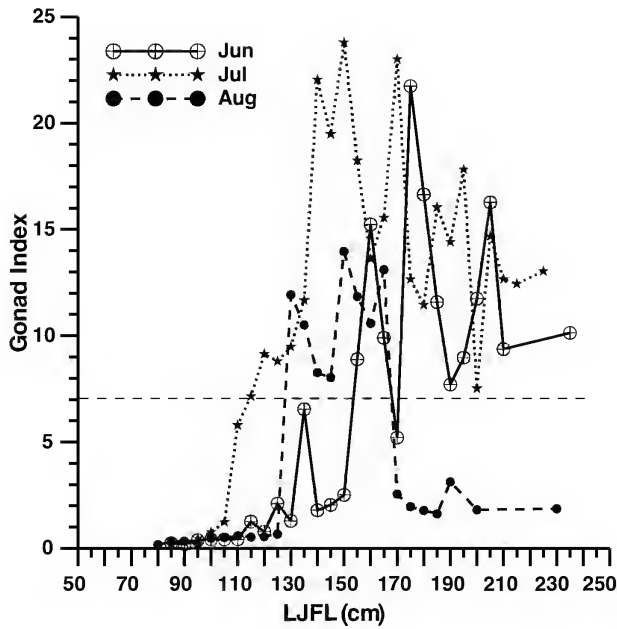


Figure 6. Western Mediterranean swordfish female monthly gonad index by size (lower jaw-fork length, LJFL) during the spawning season. Dashed line represents the spawnGI value of 7.0 (after de la Serna et al 1996).

temperature requirements favourable to their physiological demand. Therefore, during the boreal winter their bioenergetics requirements may be fulfilled in the Caribbean island passages and the shelf breaks of Venezuela, GOM and along the US southeast coast due to substantial concentrations of squid resources and meso-pelagic prey species in these areas (Boyle 1987, Stromme and Saetersdal 1989, Hopkins et al. 1996, Flanning et al. 2006). In addition, spawning females seem to prefer waters with temperatures of 24° C and 25° C at depths between 0 and 150 m

(Arocha 1997). Conversely, historical collections of larvae presumed to be a month old collected in the subtropical area were associated to similar depths and temperatures (Tåning 1955, Markle 1974, Govoni et al. 2000) as those of the spawning females. Consequently, the absence of spawning females in the temperate area is most likely due to unsuitable conditions for swordfish larvae to survive the cooled waters of the Gulf Stream as it moves north of 35°N (Gaylord and Gaines 2000). In contrast, in the tropical area where some spawning activity was observed, it appears to be a nursery area downstream from the open water spawning group of the western North Atlantic.

Swordfish in the Mediterranean Sea have a distinct spawning season. They begin to spawn in June and by the end of August most fish have spawned. Peak spawning occurred from late June to July throughout the Mediterranean spawning grounds on the basis of seasonal changes in gonad development (de la Serna et al. 1996, Corriero et al. 2004) and spawning dates obtained from aged juvenile fish (Megalofonou et al. 1995). Additionally, abundant eggs and larvae are only present in July (Cavallaro et al. 1991, Potoschi et al. 1994) and juvenile fish are common in commercial catches from September to February (Di Natale et al. 2002). All spawning took place within the Mediterranean Sea and seemed to be restricted to the area between 35° and 40°N. There was no indication that swordfish spawned west of Gibraltar, in the Adriatic or the Black Sea. In the waters off Tunisia and south of Malta, all fish caught during the spawning season were immature or spawned out (Macías et al. 2005).

Spawning in the Mediterranean seems to be associated to movements between winter-feeding grounds in Moroccan Atlantic waters and the waters west of the Strait of Gibraltar (out to 15°W) in the eastern North Atlantic

TABLE 5

Maturity fraction models, parameter estimates at size (lower jaw-fork length) and age in years (only for western North Atlantic), estimates of first maturity, 50% maturity (M_{f50}), full maturity, and sample size of fish (n) for each swordfish stock in the Atlantic Ocean. ¹Arocha 1997, ²Hazin et al. 2002, ³de la Serna et al. 1996.

Unit Stock	Model	Parameters	First maturity	M_{f50}	Full maturity	n
¹ North Atlantic	$M_f = \frac{1}{1 + e^{-a(x_i - b)}}$	Size: $a=0.151$; $b=178.73$	Size: 150.0 cm	Size: 178.7 cm	Size: 209.3 cm	Size: 470
		Age: $a=1.236$; $b=5.03$	Age: 4.0	Age: 5.03	Age: 8.7	Age: 184
² South Atlantic	$M_f = \frac{1}{1 + e^{(a+b \cdot Length)}}$	$a=11.724$; $b=-0.075$	125.0 cm	156.0 cm	195.0 cm	127
³ Mediterranean	$M_f = \frac{1}{1 + e^{-a(Length-b)}}$	$a=0.073$; $b=142.2$	110.0 cm	142.2 cm	200.0 cm	223

TABLE 6

Batch fecundity models, parameter estimates at size (lower jaw-fork length), and age in years (only for western North Atlantic), sample size of fish (n), mean batch fecundity (\bar{B}_f), batch fecundity range, and fish size and age range for each swordfish stock in the Atlantic Ocean, F_0 = minimum initial fecundity that is present when first start hydrating oocytes, and r^2 = coefficient of determination. ¹Arocha 1997, ²Hazin et al. 2001, ³de la Serna et al. 1996.

Unit Stock	Model	Parameters	r^2	n	\bar{B}_f	\bar{B}_f range	Size/Age range
		Size: $F_0 = 1757430$; $a = 11.5748$; $b = 2.8814$	Size: 0.725	Size: 29	Size: $3.91 \cdot 10^6$	0.99–9.00 · 10 ⁶	Size: 155–251 cm
¹ North Atlantic	$B_f = F_0 + a \cdot \text{Length}^b$ $B_f = F_0 + a \cdot \text{Age}^b$	Age: $F_0 = 1846990$; $a = 77.407$; $b = 4.637$	Age: 0.781	Age: 19	Age: $3.84 \cdot 10^6$		Age: 4–12
		$a = 29.811$; $b = 0.2003$	0.978	10	$5.10 \cdot 10^6$	2.00–8.60 · 10 ⁶	160–194 cm
² South Atlantic	$B_f = a \cdot \text{Length} - b$	$a = 7.013 \cdot 10^{-3}$; $b = 3.994$	0.557	16	$5.90 \cdot 10^6$	2.14–9.91 · 10 ⁶	150–193 cm
³ Mediterranean	$B_f = a \cdot \text{Length}^b$						

and spawning grounds in the Mediterranean Sea (de la Serna and Alot 1990, Pujolar et al. 2002). Mediterranean swordfish may remain in eastern North Atlantic feeding grounds until late spring when the northward displacement of the 18° C surface isotherm can cause the return into warmer Mediterranean waters (Mejuto and Hoey 1991), and fish spawn when surface waters temperatures reach 24°–26°C (Palko et al. 1981, Cavallaro et al. 1991, Corriero et al. 2004).

In contrast, the available information on the seasonality and spawning location of South Atlantic swordfish was limited to a gonad index value that was not accompanied by biologically comprehensive analyses (West 1990). Early research on swordfish reproduction off southern Brazil (20°–28°S) suggested spawning during the first trimester of the year based on histological examination of sectioned portions of the ovary (Amorim and Arfelli 1980). However, a recent study using histological techniques (Hazin et al. 2002), observed no spawning in the southwestern equatorial Atlantic (0°–10°S), but suggested that spawning occurred further north in the area where Mejuto and García (1997) observed high incidence of females with maximum gonad indices. Larval abundance and distribution was very limited and biased due to the unsystematic and broadly spaced collections in the area (Gorbunova 1969, Ueyanagi et al. 1970, Grall et al. 1983). Nonetheless, the spatial distribution was within proximity of known spawning grounds in the western South Atlantic.

Spawning swordfish in the South Atlantic appear to be concentrated around the Equator (5°N–5°S) throughout the year when temperatures in the area remain >24° C (Carton et al. 1996, Conkright et al. 1998), suitable for spawning and survival of larvae. Similar to the western North Atlantic, movements between feeding grounds and spawning grounds seem to be associated to the southward seasonal displacement in latitude of the warm isotherms (24°–25° C). This may allow smaller and larger fish to take advantage of the southern feeding grounds in the temperate waters off Uruguay and southern Brazil during the austral summer inferred from net displacement of conventional tag-recapture information in the southwestern South Atlantic (ICCAT 2006).

Swordfish in the Atlantic Ocean have an extended spawning season over a broad area in both hemispheres, but a relatively short one and in a relatively localized area in the Mediterranean. These differences appear to be attributed to displacement of the 24°C isotherm in the northern and southern hemisphere, and its seasonal appearance in the Mediterranean. In the western Atlantic, the 24° C isotherm has an ample distribution with a spread of about 50 degrees latitude that contracts and expands seasonally in each hemisphere giving swordfish the opportunity to spawn progressively in the season and enhance survival of the larvae. In contrast, spawning swordfish in the Mediterranean have a small seasonal window of opportunity when the

24° C isotherm appears in the Mediterranean between late spring and late summer when all spawning takes place. It becomes evident that each stock in the Atlantic has developed its own reproductive strategies that have not been addressed in the present work and should be addressed in future studies.

Maturity fraction and batch fecundity

Maturity estimates for swordfish caught in the Atlantic and Mediterranean differ between unit stocks. In the western North Atlantic, females were observed to mature at larger sizes and older ages than in the South Atlantic and Mediterranean Sea.

In the western North Atlantic, Taylor and Murphy (1992) estimated a length at 50% maturity of 182 cm LJFL for females from the Straits of Florida for the period of 1977–1980, and preliminary estimate of 50% maturity from Arocha et al. (1994) was 189 cm LJFL for females spawning in the western North Atlantic in the period of 1990–1993. Arocha (1997) using maximum likelihood estimation procedure obtained an estimated length at 50% maturity of 185.4 cm LJFL for the females from the Straits of Florida used in the study of Taylor and Murphy (1992). Similarly, estimates of female age-at-maturity was 5.45 yr using least squares (Taylor and Murphy 1992), while maximum likelihood estimates for the same data set and re-estimated by Arocha (1997) were 5.6 years.

Variation in size/age-at-maturity of females from western North Atlantic for the period 1990–1995 (Arocha 1997) with respect to earlier estimates mentioned above can probably be attributed to restricted location of the sampling population, estimates based on fish caught throughout the year or during the spawning season, and different parameter estimation techniques. Thus, as a result of expanding the sampling population and considering fish from the spawning period, the estimated M_{f50} was lower in Arocha (1997) than in the earlier study (Arocha et al. 1994). Accordingly, using different parameter estimation techniques, maximum likelihood estimates of M_{f50} at size and age were higher than least squares estimates for the same data set (Taylor and Murphy 1992, Arocha 1997).

The size-at-maturity of Mediterranean swordfish is the smallest of those observed for any other breeding unit in the world. Estimated M_{f50} in the Mediterranean was 142.2 cm LJFL compared to 178.7 cm LJFL in the western North Atlantic (Arocha 1997), 156 cm LJFL in the South Atlantic (Hazin et al. 2002), 162.2 cm LJFL in the central North Pacific (DeMartini et al. 2000), 175.1 cm LJFL in the western South Pacific (Young et al. 2000), and 170 cm LJFL in the western Indian Ocean (Poisson et al. 2001). The low M_{f50} observed in the Mediterranean Sea may be a

consequence of prolonged exploitation of swordfish in the area, that dates back to more than a thousand years when subsistent harpoon and gillnet near shore fisheries started around 1000–177 B.C. and expanded in the beginning of the 19th century when fishing became more sophisticated by the introduction of motor boats and modified harpoons (Ward et al. 2000). This fishing practice involved targeting large swordfish females basking at surface waters (Sella 1911, Di Natale 1991). Consequently, the numbers of older specimens were substantially reduced as observed by the low mean size of the catches for the past 30 yr, and now the fishery relies on 2 or 3, most likely immature age classes (ICCAT-GFCM 1993, De Metrio et al. 1999). Another contributing factor may be the low genetic diversity and degree of mixing of the Mediterranean population with those of the Atlantic, that would limit gene flow with populations that are comparatively less exploited (Magoulas et al. 1993, Ward et al. 2000, Cimmaruta et al. 2006).

Female swordfish in the South Atlantic appear to mature at a size smaller than any other swordfish breeding units in the world oceans, except the Mediterranean. However, the M_{f50} estimate should be considered preliminary because samples from which the estimate was derived were limited to a localized area in the western equatorial South Atlantic where numbers of mature fish were low and the geographical location was not considered a spawning area (Hazin et al. 2002).

Estimates of batch fecundity in Atlantic swordfish appeared to be similar; all estimates approach 8–9.9 million eggs per spawn. Other studies reported lower batch fecundity estimates in the Straits of Florida and in the western Indian Ocean off Reunion Island with batch fecundity estimates of 0.9–4 million eggs (Taylor and Murphy 1992, Poisson et al. 2001), and in the western South Pacific off Australia was 1–2.5 million eggs per spawn (Young et al. 2003). These differences between batch fecundity estimates may be methodological.

Batch fecundity estimates for the different Atlantic swordfish breeding units were derived using different techniques that may have resulted in potentially biased estimations. In multiple spawning fish like swordfish, with asynchronous oocyte development and indeterminate fecundity (Arocha 2002), batch fecundity can be estimated as the number of migratory-nucleus and hydrated oocytes that have not ovulated (Hunter et al. 1985). Consequently, counts of oocytes which have not entered the final stages of maturation and/or counts from ovarian samples which had been placed in fixation liquids that cause significant shrinkage will create potential bias in batch fecundity estimates (Hunter et al. 1985). Batch fecundity estimates from the South Atlantic were based on counts that had

been placed in Gilson's fluid (Hazin et al. 2001) which causes significant shrinkage and compression of oocyte size distribution which make difficult the separation of maturing oocytes from the ones that had entered the maturation phase (Schaefer 2001). Estimated batch fecundity in Mediterranean swordfish was based on counts of oocytes > 650 μm which most likely included oocytes which had not entered the maturation phase. In Corriero et al. (2004), histological sections of oocytes with late vitellogenesis from Mediterranean swordfish averaged about 600 μm , and post vitellogenesis oocytes (which included migratory-nucleus and early hydration oocytes) averaged about 850 μm . In western North Atlantic swordfish histological sections of oocytes in late vitellogenesis can measure up to 900 μm (Arocha 2002). Batch fecundity estimates from the western North Atlantic in the Straits of Florida (Taylor and Murphy 1992, Arocha 1997) were based on counts of oocytes >750 μm , but the authors offered metrics on hydrated oocytes which included 750 μm oocytes. The Arocha (1997) study used only counts of fresh unovulated hydrated oocytes, but did not include migratory-nucleus oocytes to avoid potential bias in the estimates because the duration of the migratory-nucleus phase is unknown in swordfish. In tropical tuna species where the duration of migratory-nucleus phase is known, counts of migratory-nucleus and hydrated oocytes have been used to estimate batch fecundity because the migratory-nucleus phase and hydration occurs over a short period of time (Schaefer 1998, 2001).

Batch fecundity increases with size and age, but there are few studies with size/age relationships. Linear relationships were estimated when a low number of samples were available (Hazin et al. 2001, Poisson et al. 2001, Young et al. 2003), but when the number of samples increased the relationship was nonlinear (Arocha 1997, de la Serna et al. 1996). Most swordfish batch fecundity estimates were based on studies over a relatively localized area during 2–3 yr of sampling. In contrast, batch fecundity estimates for the western North Atlantic were from a broad area over a period of 5 yr (Arocha 1997). Thus, it is probable that estimates of batch fecundity from several spawning periods may result in potential biased estimates. Schaefer (1998) found significant interannual variability in batch fecundity of *Thunnus albacares* of similar size and from the same geographical location. Similar results have been found in fish species whose reproductive biology has been investigated intensively such as *Engraulis mordax* (Hunter et al. 1985).

The combined use of gonad indices and maximum size oocytes calibrated with histological information proves to be an efficient method to define temporal and spatial

spawning patterns in non-schooling large pelagic fish like swordfish. Estimating the fraction of the population that matures assumes that specimens can be accurately classified as immature or mature. It is critical that the techniques to classify a female as sexually mature, with the use of ovary weight and/or egg size, be precise and validated, and to reduce the chance of misclassifying mature females it is recommended to limit the analysis to data collected during the spawning period. Further, the use of statistical estimation procedures that take into consideration the binomial nature of the maturity data should be considered. The estimates of batch fecundity in non-schooling large pelagic fish are complicated by the inadequate gonad sample size that can be resolved with scientific observers or trained fishers to collect samples during the spawning season. The variation in batch fecundity estimates due to estimation techniques can be resolved by using counts of unovulated hydrated oocytes.

The variation observed in the reproductive estimates, gonad indices and population parameters were mostly attributed to methodological techniques that can be corrected in future studies. The seasonality and spawning location in swordfish can be efficiently accomplished by sampling of ovarian tissues from adult specimens from commercial and recreational fisheries to map the temporal and spatial spawning distribution of swordfish. Additionally, larval surveys targeting swordfish in selected locations and specific times can provide fine-scale information on spawning. However, this technique is inefficient for large-scale spawning estimations.

The reproductive information for Atlantic swordfish presented illustrates the limited knowledge on the species, regardless of the available information for the western North Atlantic swordfish. All recent studies have been produced using data collected in the 1990s. Thus, considering there are no new comprehensive studies on reproductive dynamics, the temporal and spatial spawning patterns as well as the reproductive population parameter estimates are likely outdated. Consequently, there is a need to re-estimate and expand them, particularly for the South Atlantic stock. Future estimates should consider large-scale temporal and spatial spawning variability that would enhance the estimation of reproductive population parameters for all swordfish stocks in the Atlantic Ocean.

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Enric Cortes

National Marine Fisheries Service

Craig A. Brown

National Marine Fisheries Service

Lawrence R. Beerkircher

National Marine Fisheries Service

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RELATIVE ABUNDANCE OF PELAGIC SHARKS IN THE WESTERN NORTH ATLANTIC OCEAN, INCLUDING THE GULF OF MEXICO AND CARIBBEAN SEA

Enric Cortés¹, Craig A. Brown², and Lawrence R. Beerkircher²

¹National Marine Fisheries Service, Panama City Laboratory, 3500 Delwood Beach Road, Panama City, Florida 32408 USA, E-mail enric.cortez@noaa.gov

²National Marine Fisheries Service, Southeast Fisheries Science Center, 75 Virginia Beach Drive, Miami, Florida 33149 USA

ABSTRACT Little information exists on the status of pelagic shark populations in the Atlantic Ocean, especially in the Gulf of Mexico and Caribbean Sea. We derived indices of relative abundance for pelagic sharks based on mandatory logbooks and observer reports from a scientific observer program of the United States (US) pelagic longline fleet. Time series data from the pelagic longline logbook program (1986–2005) and the pelagic longline observer program (1992–2005) were standardized with Generalized Linear Model (GLM) procedures. Declines in relative abundance for the 6 pelagic shark species or genera examined in the logbook data analysis ranged from 43% for mako sharks, *Isurus* spp., to 88% for blue sharks, *Prionace glauca*, whereas declines in relative abundance obtained from the observer data analysis were less accentuated than those in the logbook data analysis, with the trend being positive for night sharks, *Carcharhinus signatus*, and thresher sharks, *Alopias* spp. There was no significant change in the fork length at capture over the time period considered for blue sharks, shortfin makos *Isurus oxyrinchus*, or night sharks. The trends obtained must be viewed cautiously given recognized shortcomings, especially of the logbook dataset, and the highly migratory nature of pelagic sharks, which requires a more comprehensive evaluation of trends throughout their range.

RESUMEN Existe poca información sobre el estado de las poblaciones de tiburones pelágicos en el Océano Atlántico, especialmente en el Golfo de México y el Mar Caribe. Derivamos índices de abundancia relativa para tiburones pelágicos a partir de cuadernos de bitácora e informes de observadores de un programa de observadores científicos de la flota palangrera pelágica de los Estados Unidos (EE.UU.). Las series temporales del programa de cuadernos de bitácora de palangre pelágico (1986–2005) y del programa de observadores de palangre pelágico (1992–2005) se estandarizaron por medio de Modelos Lineales Generalizados (GLMs). Las reducciones en abundancia relativa de las seis especies o géneros de tiburones pelágicos que se examinaron variaron entre el 43% para *Isurus* spp. y el 88% para *Prionace glauca*, mientras que los descensos en abundancia relativa obtenidos del análisis de los datos de observadores fueron menos acentuados que los del análisis de los datos de los cuadernos de bitácora, con *Carcharhinus signatus* y *Alopias* spp. mostrando tendencias positivas. No se encontraron cambios significativos en la longitud furcal de las capturas durante el período analizado para *P. glauca*, *Isurus oxyrinchus* o *C. signatus*. Las tendencias obtenidas deben interpretarse con cautela debido a distintos problemas, en especial con los cuadernos de bitácora, y el hecho de que los tiburones pelágicos son altamente migratorios, lo cual requiere una evaluación más exhaustiva de las tendencias que abarque todo el rango de distribución de estas especies.

INTRODUCTION

There is mounting concern about the status of pelagic shark populations worldwide. While it is widely recognized that many populations in the Atlantic Ocean have experienced substantial declines with respect to virgin (unexploited) levels, the extent of these declines has been the subject of intense debate (Baum et al. 2003, Baum and Myers 2004, Burgess et al. 2005a,b, Baum et al. 2005).

Pelagic sharks are often trans-oceanic species and are harvested or caught as bycatch by fishers from several nations. Although it has long been recognized that assessment of pelagic shark resources requires a multinational approach, the first assessment of 2 pelagic shark species (shortfin mako, *Isurus oxyrinchus*, and blue shark, *Prionace glauca*) in the Atlantic Ocean did not take place until 2004,

under the auspices of the International Commission for the Conservation of Atlantic Tunas (ICCAT). That assessment, which was considered very preliminary owing to the limitations of both the quantity and quality of information available, concluded that stock biomass of both North and South Atlantic blue sharks was likely above Maximum Sustainable Yield (MSY), whereas the North Atlantic stock of shortfin mako could be below biomass at MSY, with the magnitude of the decline for the shortfin mako stock in the South Atlantic estimated to be less than in the North Atlantic stock (ICCAT 2005).

Three species of pelagic sharks, the bigeye thresher, *Alopias superciliosus*, longfin mako, *Isurus paucus*, and the night shark, *Carcharhinus signatus*, have been prohibited to fisheries in Northwest Atlantic US waters since 2000 (NMFS 2003). In 1997, the night shark was also des-

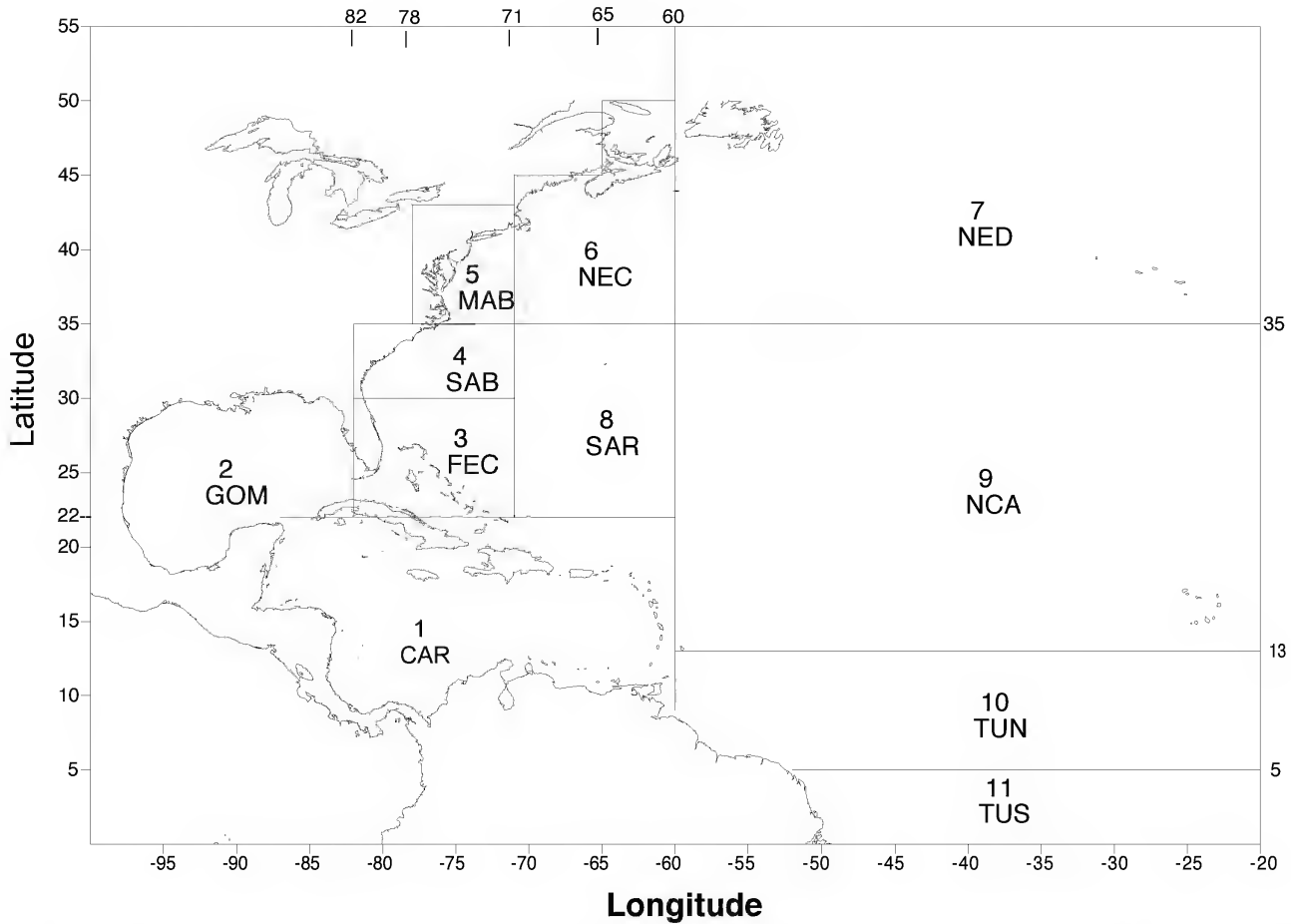


Figure 1. Map of the western North Atlantic Ocean. Areas are as follows: 1) Caribbean Sea (CAR), 2) Gulf of Mexico (GOM), 3) Florida East coast (FEC), 4) South Atlantic Bight (SAB), 5) Mid-Atlantic Bight (MAB), 6) New England coastal (NEC), 7) Northeast distant waters (NED or Grand Banks), 8) Sargasso Sea (SAR), 9) North Central Atlantic (NCA), 10) Tuna North (TUN), and 11) Tuna South (TUN).

ignated by the National Marine Fisheries Service (NMFS) as a candidate species under the Endangered Species Act (ESA). On a global scale, the World Conservation Union (IUCN) Red List of Threatened Species classified the blue shark, shortfin mako, oceanic whitetip shark, *Carcharhinus longimanus*, and porbeagle, *Lamna nasus*, as near threatened, the thresher shark, *Alopias vulpinus*, as data deficient (but the California population as near threatened), and the silky shark, *Carcharhinus falciformis*, of least concern (pending an update), whereas the bigeye thresher, longfin mako, and night shark were not yet listed (Fowler et al. 2005).

Given the general paucity of data on the status of pelagic shark populations, especially in the Gulf of Mexico (GOM) and Caribbean Sea (CAR), we developed or updated time series of relative abundance for a variety of species based both on mandatory logbooks and observer reports from a scientific observer program of the US pelagic long-

line fleet. Additionally, we examined trends in length of the main species for possible signs of overexploitation.

MATERIALS AND METHODS

Data

The pelagic longline fishing grounds for the US fleet extend from the Grand Banks (about 45°N) in the North Atlantic to 5–10°S, off the South American coast, including the CAR and the GOM. Eleven geographical areas of longline fishing are defined for classification (Figure 1): the CAR (area 1), GOM (area 2), Florida East coast (FEC, area 3), South Atlantic Bight (SAB, area 4), Mid-Atlantic Bight (MAB, area 5), New England coastal (NEC, area 6), Northeast distant waters (NED, or Grand Banks, area 7), Sargasso Sea (SAR, area 8), North Central Atlantic (NCA, area 9), Tuna North (TUN, area 10), and Tuna South (TUN, area 11).

Data from the US pelagic longline logbooks were available for 1986–2005, and sufficient information to develop time series (here forth referred to as logbook index) was available for blue, mako (the sum of shortfin and longfin makos), thresher (the sum of common and bigeye threshers), silky, oceanic whitetip, and night sharks. Initially, we attempted to include all areas in the analysis, but in some cases we had to restrict the dataset to certain areas owing to insufficient or unbalanced observations by year in the remaining areas. Thus, we only included areas 2, 3, 4, and 5 for silky and night sharks, and areas 1, 2, 3, 4, and 8 for oceanic whitetip sharks. We also developed time series (here forth referred to as restricted logbook index) for areas 1 and 2 only (GOM and CAR).

Data from the US pelagic longline observer program were available for 1992–2005, and information to develop time series (here forth referred to as observer index) was also available for blue, mako (the sum of shortfin, longfin, and unidentified makos), thresher (the sum of common, bigeye, and unidentified threshers), silky, oceanic whitetip, and night sharks. As for the logbook analyses, we initially attempted to include all areas, but had to restrict the dataset to certain areas in all cases. Thus, for mako sharks we included areas 2, 4, 5, 6, and 7 only, areas 2, 3, 4, and 5 for silky, night, and thresher sharks, areas 1, 2, 3, and 4 for oceanic whitetip sharks, and areas 5, 6, and 7 for blue sharks. No analyses were conducted using areas 1 and 2 only owing to small sample sizes.

Based on the methodology used in Brooks et al. (2005) and Cortés (2006), the following factors were considered in the analyses: year, area, quarter (January–March, April–June, July–September, October–December), gear (bottom longline or pelagic longline), presence or absence of light sticks, and whether or not the data were part of experimental fishing (conducted in years 2000–2003 in the northeast distant area [7] only). Additionally, nominal catch rates (catch per thousand hooks) of swordfish, *Xiphias gladius*, and tuna (the sum of albacore, *Thunnus alalunga*, skipjack, *Euthynnus pelamis*, bigeye, *Thunnus obesus*, and yellowfin, *Thunnus albacares*) were calculated for each set, and a categorical factor based on the quartile of those catch rates was assigned to each set (the factors are denoted as Sqr and Tqr, respectively). The reason for creating these factors, which correspond to the <25%, 25–49%, 50–75%, and >75% quantiles of the proportion, was to attempt to control for effects of pelagic shark catch rates associated with changes of fishing operations when the fleets switch between targeted species. We also considered the following interactions: year*area, year*quarter, year*gear, gear*area, as well as the interactions between area and the nominal catch rate quartiles for tuna and swordfish (area*Sqr and

area*Tqr). Note that for the observer analysis the gear factor was not considered because all the observations included in the dataset analyzed corresponded to pelagic longline. Nominal catch rates (not statistically standardized) were defined in all cases as catch per 1000 hooks.

To examine length trends, we used records of animals that were brought onboard and measured (fork length; in a straight line) by observers from the pelagic longline observer program. No estimated lengths, which are sometimes recorded by the observers, were used. Sufficient observations, combining all areas, were only available for the blue, shortfin mako, and night sharks.

Analysis

Relative abundance indices were estimated using a Generalized Linear Modeling (GLM) approach assuming a delta lognormal model distribution. A binomial error distribution was used for modeling the proportion of positive sets with a logit function as link between the linear factor component and the binomial error. A lognormal error distribution was used for modeling the catch rates of successful sets, wherein estimated CPUE (catch per unit of effort) rates assume a lognormal distribution ($\ln\text{CPUE}$) of a linear function of fixed factors. The models were fitted with the SAS GENMOD procedure (SAS Institute Inc. 1999) using a forward stepwise approach in which each potential factor was tested one at a time. Initially, a null model was run with no explanatory variables (factors). Factors were then entered one at a time and the results ranked from smallest to greatest reduction in deviance per degree of freedom when compared to the null model. The factor which resulted in the greatest reduction in deviance per degree of freedom was then incorporated into the model if 2 conditions were met: 1) the effect of the factor was significant at least at the 5% level based on the results of a Chi-Square statistic of a Type III likelihood ratio test, and 2) the deviance per degree of freedom was reduced by at least 1% with respect to the less complex model. Single factors were incorporated first, followed by fixed first-level interactions. The year factor was always included because it is required for developing a time series. Results were summarized in the form of deviance analysis tables including the deviance for proportion of positive observations and the deviance for the positive catch rates.

Once the final model was selected, it was run using the SAS GLIMMIX macro (which uses iteratively re-weighted likelihoods to fit generalized linear mixed models with the SAS MIXED procedure; Wolfinger and O'Connell 1993, Littell et al. 1996). In this model, any interactions that included the year factor were treated as a random effect. Goodness-of-fit criteria for the final model included

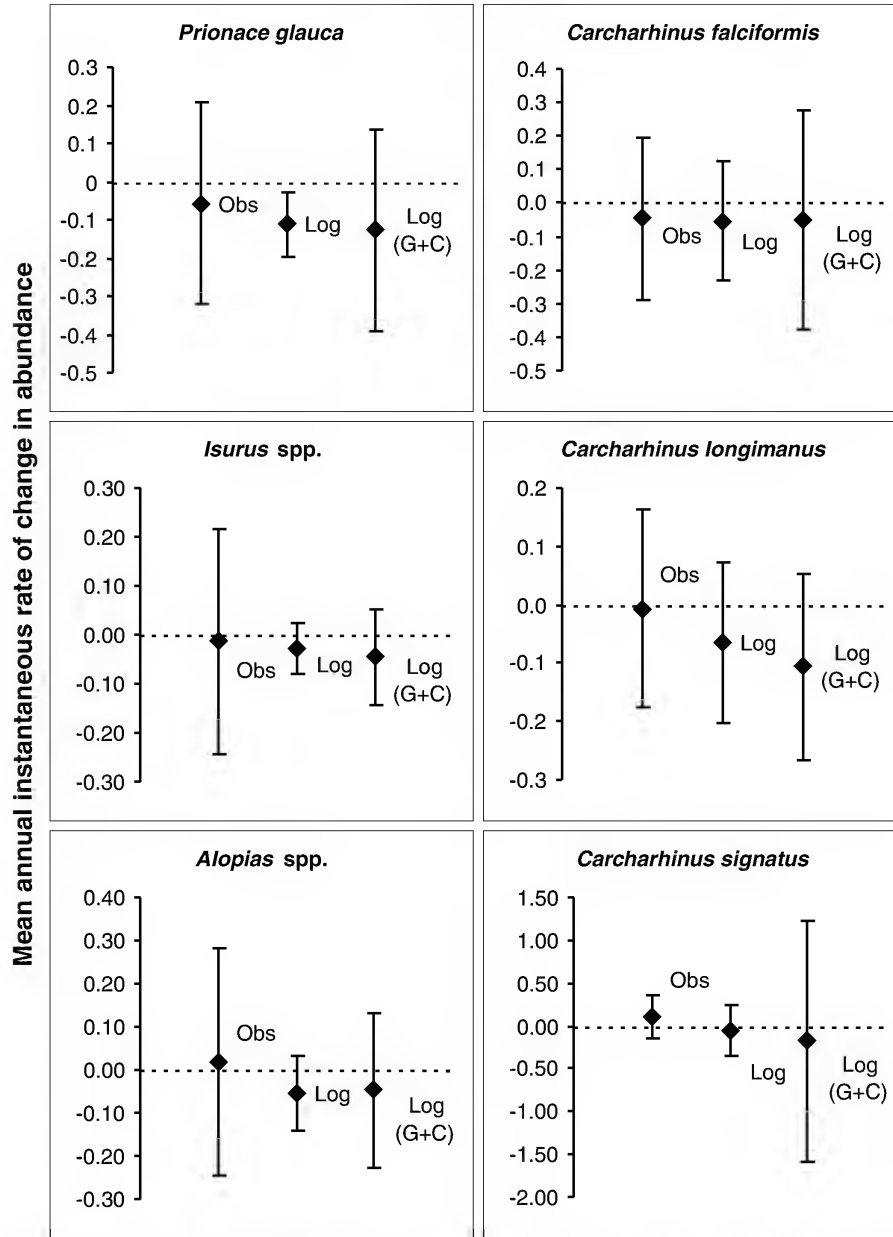


Figure 2. Estimated mean annual instantaneous rate of change in abundance ($\pm 95\%$ CL) for blue, mako, thresher, silky, oceanic whitetip, and night sharks from the pelagic longline observer (Obs), pelagic longline logbook (Log), and pelagic longline logbook data set restricted to areas 1 and 2 (Gulf of Mexico and Caribbean Sea).

Akaike's Information Criterion (AIC), Schwarz's Bayesian Criterion, and $-2 \times$ the residual log likelihood (-2Res L). The significance of each individual factor was tested with a Type III test of fixed effects, which examines the significance of an effect with all the other effects in the model (SAS Institute Inc. 1999). The final mixed model calculated relative indices as the product of the year effect least squares means (LSMeans) from the binomial and lognormal components. LSMeans estimates were weighted proportionally to observed margins in the input data, and

for the lognormal estimates, a back-transformed log bias correction was applied (Lo et al. 1992).

Logbook analysis results were compared to those from a recent analysis (Brooks et al. 2005) or from an earlier analysis (Cramer 2000) of the same source, those from the observer analysis, those from the restricted analysis of areas 1 and 2, and those from Baum et al. (2003), which also used the logbook dataset but only up to 2000. The restricted analysis for the GOM and CAR was also compared to Baum and Myers (2004), which compared sur-

TABLE 1

Factors retained in the models of proportion of positive sets and positive catch for US pelagic longline logbook and observer data by species or genus.

LOGBOOK

Species or group	Proportion positive	Positive catches
<i>Prionace glauca</i>	area Sqr year	area year quarter year*area Tqr*area year*quarter
<i>Isurus</i> spp.	area Sqr year	Tqr year area Sqr quarter year*area Tqr*area Sqr*area
<i>Alopias</i> spp.	year area	area year Sqr Tqr year*area year*quarter Sqr*area
<i>Carcharhinus falciformis</i>	area Sqr Tqr year	year Tqr area quarter year*area Tqr*area Sqr*area
<i>Carcharhinus longimanus</i>	area year year*area year*quarter	year area Sqr Tqr Sqr*area
<i>Carcharhinus signatus</i>	area Sqr year year*area year*quarter	year area Tqr year*area year*quarter

OBSERVER

Species or group	Proportion positive	Positive catches
<i>Prionace glauca</i>	area year Sqr quarter	area year quarter year*quarter year*area Tqr*area Sqr*area
<i>Isurus</i> spp.	area year Sqr experiment year*quarter year*area	year area Sqr quarter experiment Tqr year*area year*quarter Tqr*area
<i>Alopias</i> spp.	year quarter area Tqr*area	area Tqr Sqr year Sqr*area
<i>Carcharhinus falciformis</i>	area Sqr year Tqr	Tqr year Sqr area year*quarter year*area Tqr*area
<i>Carcharhinus longimanus</i>	area quarter year	year Sqr area quarter Tqr year*area Tqr*area Sqr*area
<i>Carcharhinus signatus</i>	area Sqr year year*quarter Sqr*area	year Tqr year*area year*quarter

veys conducted in the 1950s with pelagic longline observer data from the late 1990s in the GOM.

RESULTS**Catch rates**

Significant factors. In the analysis of the logbook data, factors retained for the proportion of positive sets always included year and area, and Sqr to a lesser extent, whereas for the positive catches, the factors quarter (or its interaction with year) and Sqr and Tqr (or their interaction with area) also were typically retained in addition to year and area (Table 1). For the observer data, factors retained for the proportion of positive sets also were year and area, with quarter and Sqr (or their interaction with year or area, respectively) also being generally retained,

and Tqr (or its interaction with area) to a lesser extent; for the positive catches, the factors year and area always were retained, and Sqr and Tqr (or their interaction with area), and quarter (or its interaction with year) also were generally retained (Table 1).

Trends in relative abundance

Blue sharks. The logbook index shows very good agreement with the index developed previously (Brooks et al. 2005) and an 88% decline since 1986 corresponding to a mean instantaneous rate of change in abundance per year (r) of -0.113 (95% confidence interval [CI]: -0.197 to -0.028 ; Figure 2). This decline was largely driven by a 55% decline in the first 3 years of the series (1986–1988), with 1986 having the lowest number of positive observations (sets with positive catches) in any year ($n = 568$;

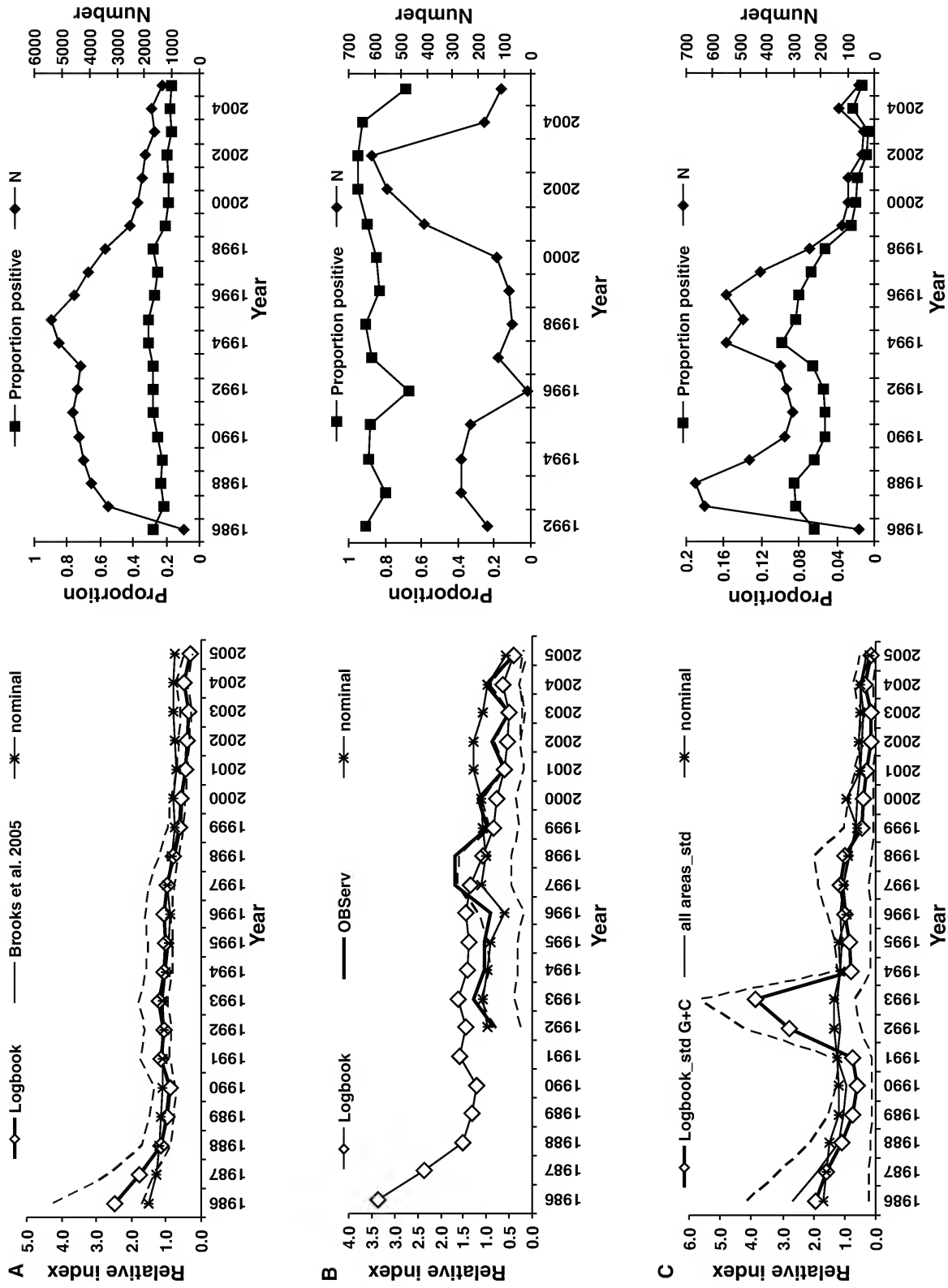


Figure 3. Nominal and standardized CPUE (in number) with 95% confidence intervals (dashed lines) for blue sharks from A) the pelagic longline logbook compared to a previous study by Brooks et al. (2005), B) the pelagic longline observer program and C) the pelagic longline logbook restricted to areas 1 and 2 (Gulf of Mexico and Caribbean Sea). All indices are standardized to the mean of the overlapping years. The right panels show the proportion of positive sets and sample size by year.

Figure 3A). From 1989 to 2005, the series slowly declined from a relative value of about 0.97 to 0.29. In contrast, the nominal series showed a flatter trend, with a relative decline of 50% from beginning to end. When removing 1986 from the standardized time series, the relative decline since 1987 was still 83%. Diagnostic plots showed good agreement with model assumptions and there were no systematic patterns in the residuals.

The observer index shows a 52% decline since 1992 ($r = -0.057$, 95% CI: -0.320 to 0.206), but larger interannual variation than the logbook index, which shows a smoother trend for the overlapping years (Figure 3B). The nominal observer series showed a 43% decline. The restricted logbook index showed a similar trend to the logbook index for all areas, with the exception of a peak in 1992–1993, but collectively showed a similar decline since 1986 (91% vs 88%; $r = -0.128$, 95% CI: -0.394 to 0.138 ; Figure 3C).

Mako sharks. The logbook index also shows very good agreement with the index developed previously (Brooks et al. 2005) and a 43% decline since 1986 ($r = -0.03$, 95% CI: -0.081 to $+0.022$; Figure 2). This decline was largely driven by a 21% decline in the first 3 years of the series (1986–1988), followed by an increase in 1989, and a progressive decline from 1989 to 1999, after which the series progressively started increasing until 2005 (Figure 4A). As with the blue shark, 1986 had the lowest number of positive observations for any year ($n = 354$). The nominal series also had a concave, but somewhat flatter trend, with lower initial and final values and a relative decline of 36% from beginning to end. When removing 1986 from the standardized time series, the relative decline was essentially the same as when including 1986 (43%). Diagnostic plots showed good agreement with model assumptions and there were no systematic patterns in the residuals.

The observer index shows a 15% decline since 1992 ($r = -0.012$, 95% CI: -0.243 to 0.218), but larger interannual variation than the logbook index, which shows a smoother trend for the overlapping years (Figure 4B). The trends of both indices are similar, however. The nominal observer series showed a 34% decline. The restricted logbook index showed a trend relatively similar to the logbook index for all areas until 1999, but was reversed for 2000–2005. Collectively, it showed a larger decline since 1986 (57% vs 43%; $r = -0.045$, 95% CI: -0.142 to 0.053 ; Figure 4).

Thresher sharks. The logbook index trend is similar to that developed previously (Cramer 2000) and shows a 63% decline since 1986 ($r = -0.053$, 95% CI: -0.139 to $+0.033$; Figure 2). With the exception of the first and

last year of data (1986 and 2005, respectively), the trend declined (Figure 5A). The number of positive observations for the latter part of the time series (2001–2005, $n < 400$), and especially for 1986 ($n = 112$), was lower than for the remaining years. The nominal series showed a less pronounced slope, with a relative decline of 46% from beginning to end. Diagnostic plots showed good agreement with model assumptions and there were no systematic patterns in the residuals.

The observer index shows a trend opposite to that of the logbook analysis, with a 28% increase since 1992 ($r = 0.019$, 95% CI: -0.246 to 0.284); the index from the logbook analysis for the same period of coverage (1992–2005) shows a decrease of 50% (Figure 5B). The number of positive observations in the observer analysis, however, was much smaller ($n = 14$ – 84) than that in the logbook analysis ($n = 112$ – 1292). In contrast, the nominal observer series showed a 39% decline. The restricted logbook index showed a similar trend to the logbook index for all areas, with a 59% decrease since 1986 ($r = -0.047$, 95% CI: -0.228 to 0.133 ; Figure 5C). The trend, however, was less precise as a result of the lower sample size.

Silky sharks. The logbook index shows a similar, but smoother, decreasing trend as developed previously (Cramer 2000) and a 50% decline since 1992 ($r = -0.054$, 95% CI: -0.233 to 0.126 ; Figure 2). This decline was largely driven by a 61% decline in 1992–1998, followed by a generally increasing tendency from 1998 to the end of the time series (Figure 6A). In contrast to some of the cases examined above, the number of positive observations for the period where the sharpest decline in catch rates occurred was actually the largest ($n = 703$ – 952). The nominal series also showed a generally declining trend, with a 38% decrease since 1992. Diagnostic plots showed good agreement with model assumptions and there were no systematic patterns in the residuals.

The observer index shows a similar decline since 1992 to that in the logbook data (46% vs 50%), but larger interannual variation ($r = -0.047$, 95% CI: -0.290 to 0.197 ; Figures 2B and 6). The nominal observer series showed a 40% decline from beginning to end. The restricted logbook index showed a similar trend to that of the logbook index for all areas, with an initial decrease from 1992 to 1998, followed by an increasing tendency from 1998 to 2005. The logbook index for all areas, however, was much smoother than the restricted index, which still showed a decline of the same magnitude since 1992 (48% vs 50%; $r = -0.051$, 95% CI: -0.377 to 0.275 ; Figure 6C).

Oceanic whitetip sharks. The logbook index shows a similar trend to that developed previously (Cramer 2000), except for a higher value in the first year of data (1992),

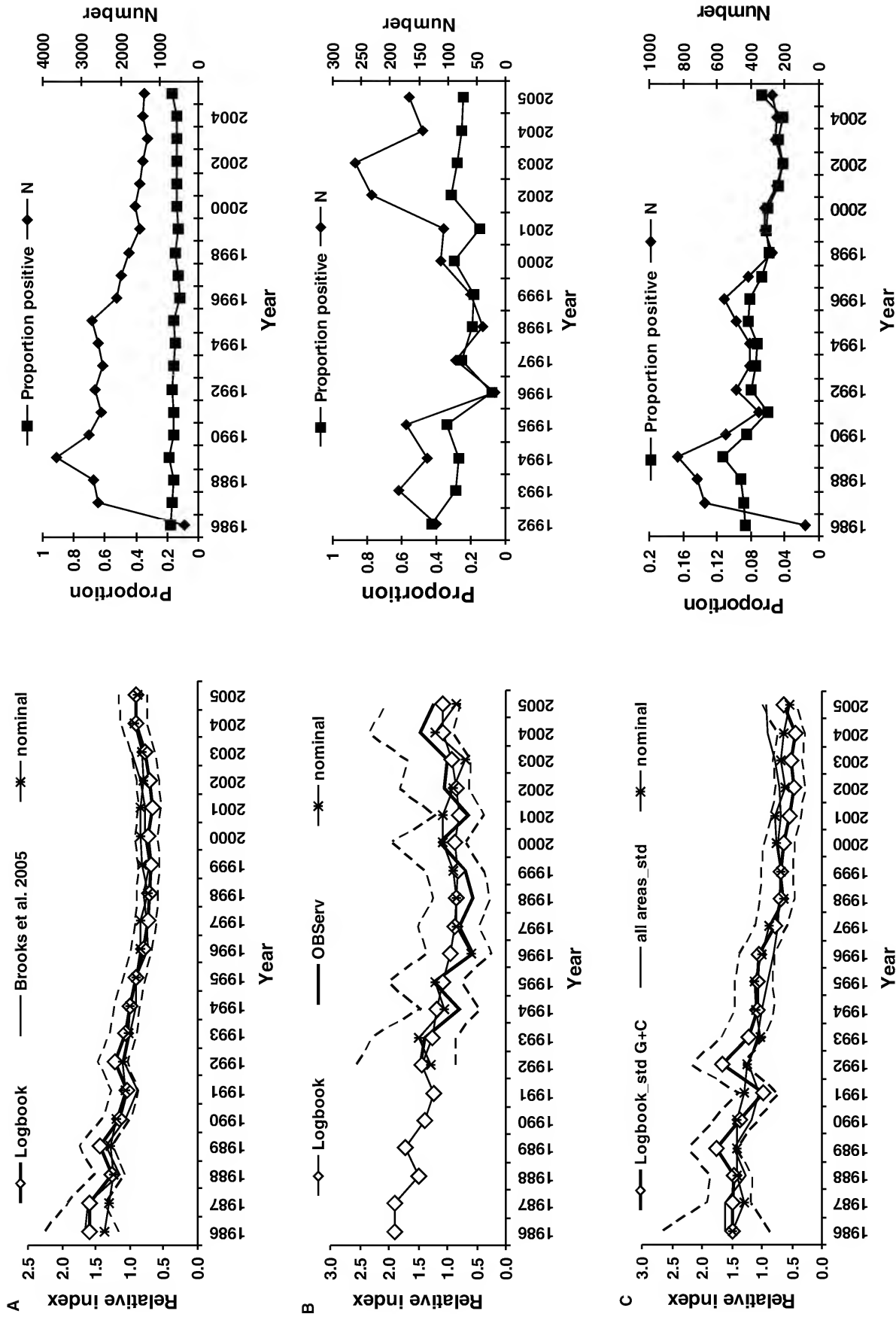


Figure 4. Nominal and standardized CPUE (in number) with 95% confidence intervals (dashed lines) for mako sharks from A) the pelagic longline logbook compared to a previous study by Brooks et al. (2005), B) the pelagic longline observer program and C) the pelagic longline logbook restricted to areas 1 and 2 (Gulf of Mexico and Caribbean Sea). All indices are standardized to the mean of the overlapping years. The right panels show the proportion of positive sets and sample size by year.

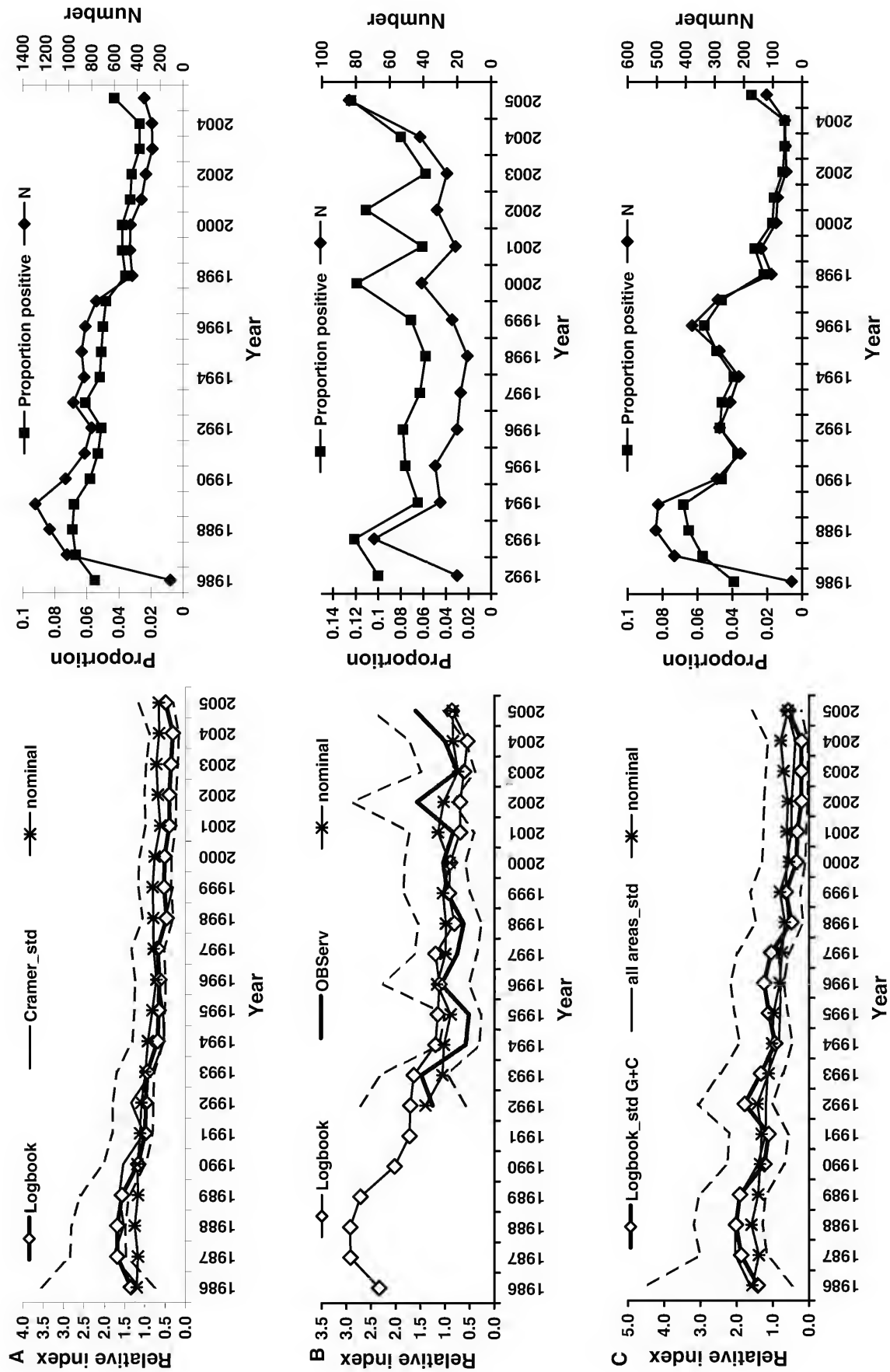


Figure 5. Nominal and standardized CPUE (in number) with 95% confidence intervals (dashed lines) for thresher sharks from A) the pelagic longline logbook compared to a previous study by Cramer (2000), B) the pelagic longline observer program and C) the pelagic longline logbook restricted to areas 1 and 2 (Gulf of Mexico and Caribbean Sea). All indices are standardized to the mean of the overlapping years. The right panels show the proportion of positive sets and sample size by year.

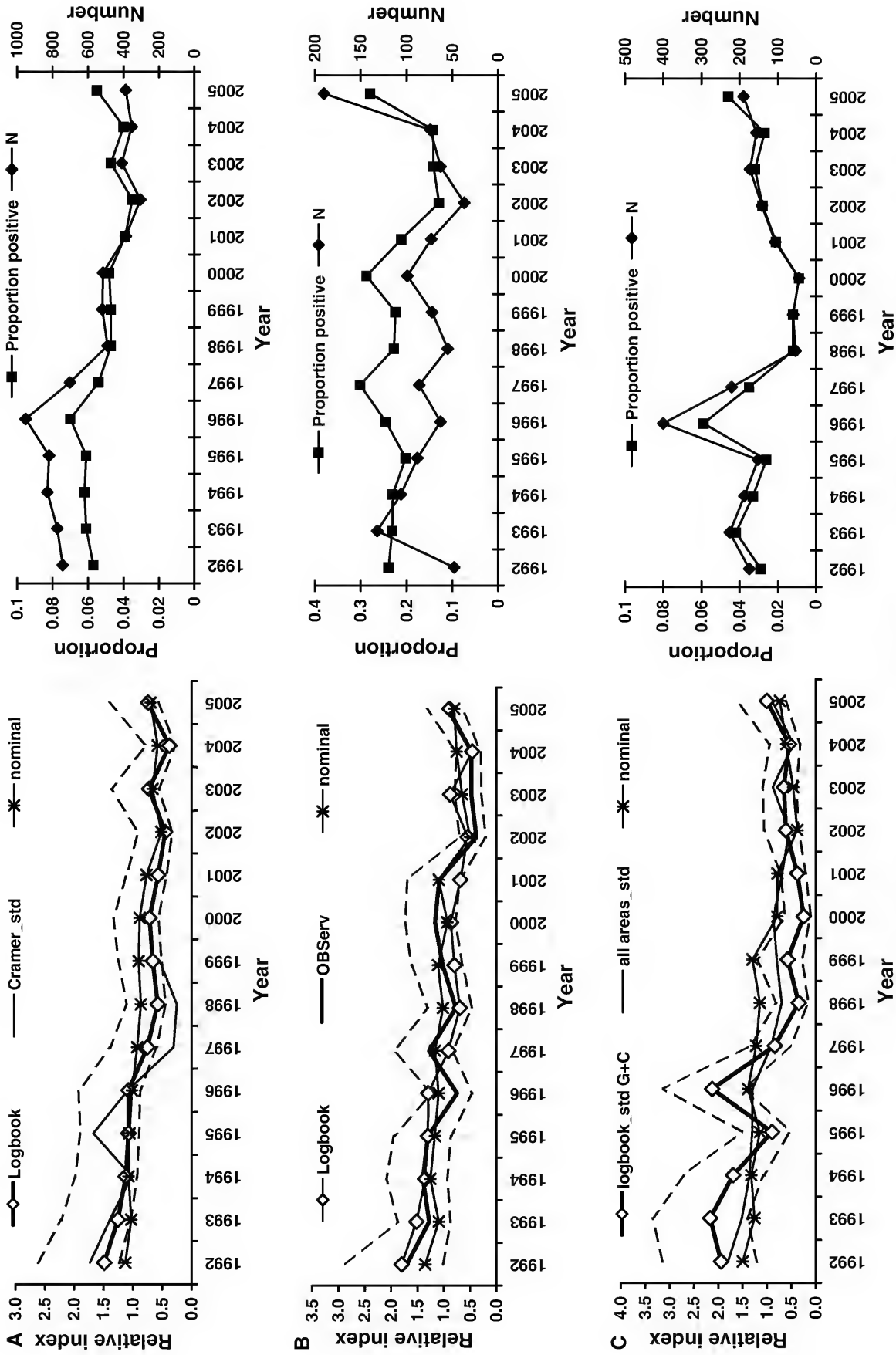


Figure 6. Nominal and standardized CPUE (in number) with 95% confidence intervals (dashed lines) for silky sharks from A) the pelagic longline logbook compared to a previous study by Cramer (2000), B) the pelagic longline observer program and C) the pelagic longline logbook restricted to areas 1 and 2 (Gulf of Mexico and Caribbean Sea). All indices are standardized to the mean of the overlapping years. The right panels show the proportion of positive sets and sample size by year.

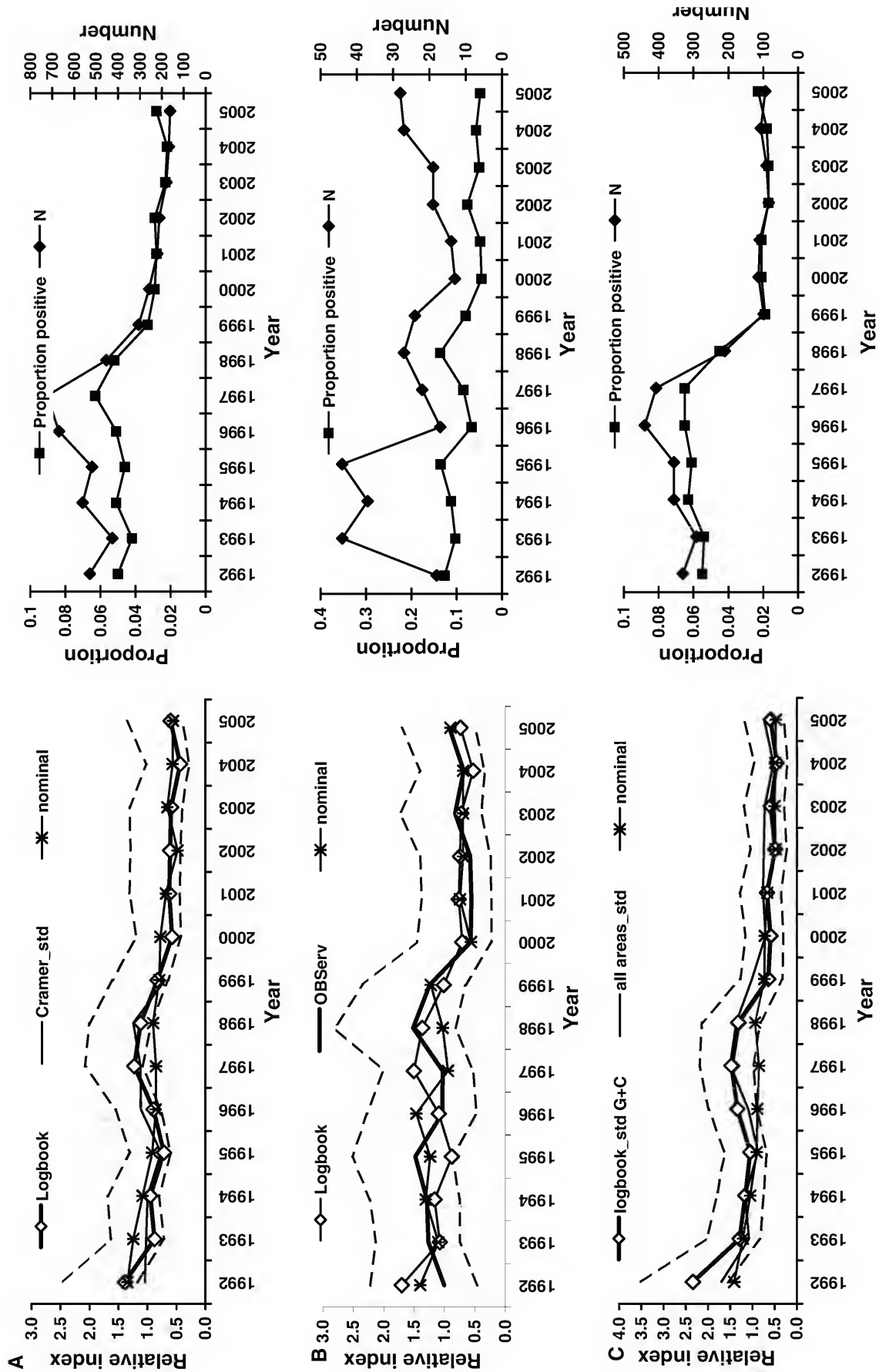


Figure 7. Nominal and standardized CPUE (in number) with 95% confidence intervals (dashed lines) for oceanic whitetip sharks from A) the pelagic longline logbook compared to a previous study by Cramer (2000), B) the pelagic longline observer program and C) the pelagic longline logbook restricted to areas 1 and 2 (Gulf of Mexico and Caribbean Sea). All indices are standardized to the mean of the overlapping years. The right panels show the proportion of positive sets and sample size by year.

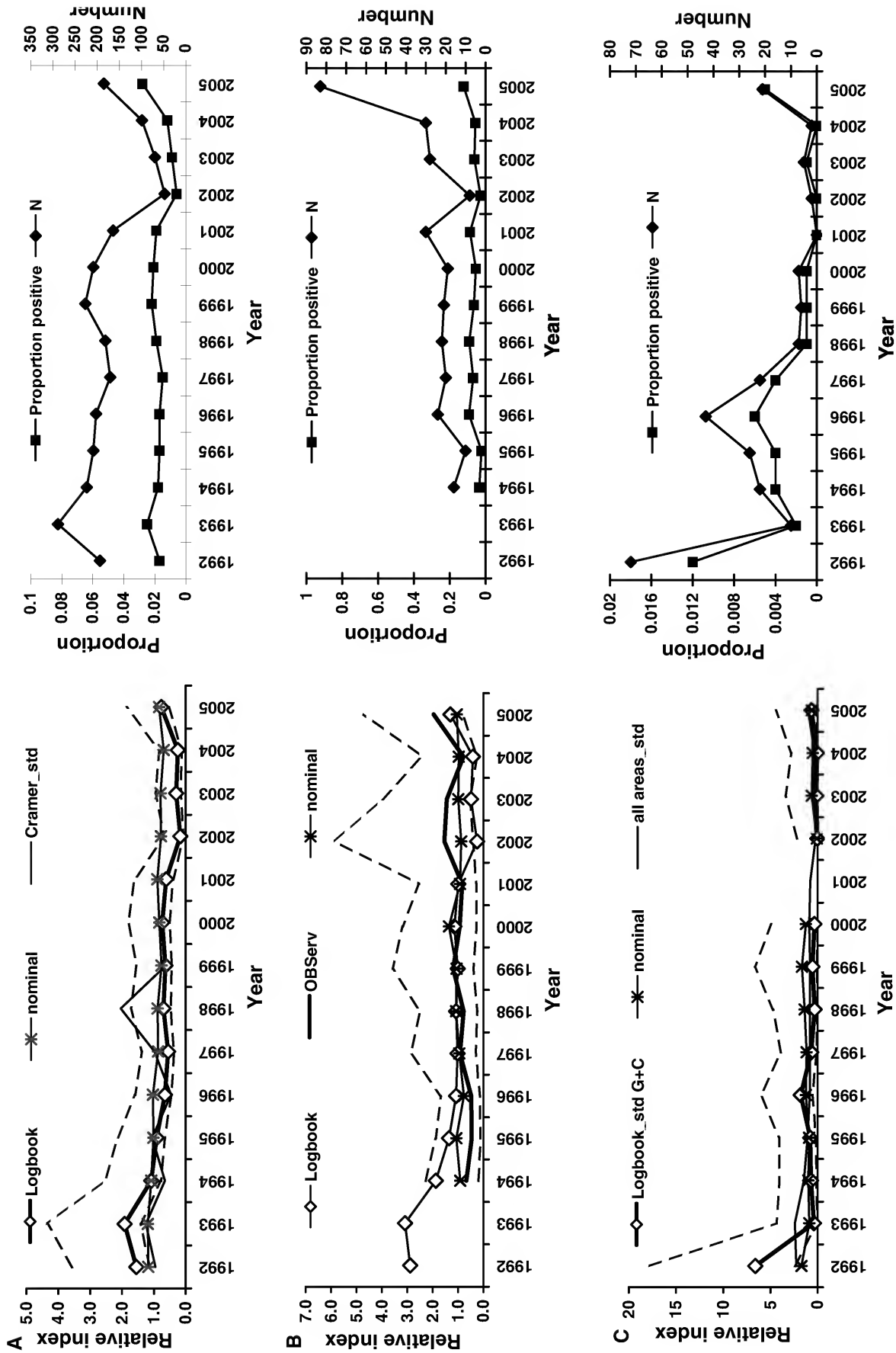


Figure 8. Nominal and standardized CPUE (in number) with 95% confidence intervals (dashed lines) for night sharks from A) the pelagic longline logbook compared to a previous study by Cramer (2000), B) the pelagic longline observer program and C) the pelagic longline logbook restricted to areas 1 and 2 (Gulf of Mexico and Caribbean Sea). All indices are standardized to the mean of the overlapping years. The right panels show the proportion of positive sets and sample size by year.

which results in a much steeper decline from 1992 to 1993 (Figure 7A). Overall, the series shows a 57% decline since 1992 ($r = -0.064$, 95% CI: -0.202 to 0.073 ; Figure 2). The decline was largely driven by a 37% decline from 1992 to 1993, and a subsequent decline of 53% from 1997 to 2000, after which the time series remained stable (2000–2005). The number of positive observations progressively dropped after 1997. The nominal series also showed a generally declining trend, with a 59% decrease since 1992. Diagnostic plots showed good agreement with model assumptions and there were no systematic patterns in the residuals.

The observer index shows a less pronounced decline than the logbook series (9% vs 57%; $r = -0.007$, 95% CI: -0.176 to 0.162 ; Figure 7B), while the nominal observer series showed a 36% decline since 1992. The restricted logbook index matched fairly well the logbook index for all areas, but showed a larger decline (75% vs 57%; $r = -0.106$, 95% CI: -0.266 to 0.053 ; Figure 7C).

Night sharks. The logbook index differs substantially from that reported previously (Cramer 2000), showing a 50% decline since 1992 ($r = -0.054$, 95% CI: -0.354 to 0.246 ; Figure 2). Several sub-trends can be identified in the time series: an initial decrease from 1993 to 1997 (after an increase from 1992–1993), followed by a rather flat trend from 1997 to 2001 and a dip in 2002, and an increasing tendency towards the end of the time series (2002–2005), although the number of positive observations in 2002–2004 was lower than for the remaining years (Figure 8A). The nominal series showed a generally flatter trend, with a 29% decrease since 1992. Diagnostic plots showed good agreement with model assumptions and there were no systematic patterns in the residuals.

The observer index shows a totally different trend to that of the logbook data for the overlapping years (1994–2005), increasing by 192% since 1994 ($r = 0.097$, 95% CI: -0.153 to 0.348 ; Figure 8B). The nominal observer series showed a much flatter trend, with a 14% overall increase. The restricted logbook index showed a much more accentuated decline than the logbook index for all areas (90% vs 55%; $r = -0.179$, 95% CI: -1.588 to 1.230 ; Figure 8C), but it was largely driven by a very steep decline from 1992 to 1993 (1992 had the largest sample size of any year; $n = 72$). The restricted logbook index showed many fluctuations, and was based on low sample size, with no positive observations in 2001 and less than 10 positive observations in multiple years.

Trends in size

There was no clear trend in fork length over the time period considered for any of the 3 species examined

(Figure 9). The correlation between fork length and year was very low in all cases ($r \leq 0.042$) and the regression was not statistically significant, except for the blue shark, which showed a statistically significant negative slope ($P = 0.007$).

DISCUSSION

Declines in relative abundance for the 6 pelagic shark species or genera examined in the logbook analysis ranged from 43% for mako sharks to 88% for blue sharks (Table 2). Despite smaller sample sizes leading to more uncertain trends and larger interannual variation in the logbook analysis restricted to the Gulf and Caribbean region, declines agreed very well with those of the full logbook analysis for blue, thresher, and silky sharks, whereas the magnitude of the difference in predicted declines progressively increased for mako, oceanic whitetip, and night sharks. With the exception of silky sharks, changes in relative abundance obtained from the observer analysis were very different from those in the logbook analysis. The trend using observer data was highly positive for night sharks, and thresher sharks to a lesser extent. As was the case for the restricted logbook analysis, sample sizes were lower, the corresponding trends more uncertain, and interannual fluctuation more accentuated in the observer analysis.

Some of the index values particularly in the restricted logbook analyses may not be reflective of true population abundance. A good example is the peak in 1992 and 1993 for blue sharks, which is not the result of low sample size, but could be due to increased local availability as a result of a larger portion of the stock moving through the area during those years. Since catch rates in the restricted logbook analysis are generally lower than in the full logbook analysis (about an order of magnitude for blue sharks), the addition of a few more blue sharks in 1992 and 1993 could explain the observed peaks.

While the full logbook analysis had much larger sample sizes than the observer analysis, which generally covers 3–5% of the total number of sets, and thus is better to estimate trends with more certainty, species identification and reporting is much better in the observer program than in the logbook program. From an identification perspective, the most problematic species for observers would be the silky and night sharks, which can be confused with each other and the dusky shark, *Carcharhinus obscurus*. The increasing trend in night sharks estimated from the observer analysis could be related to progressively better observer skills in identifying night sharks, which only started to be recorded in 1994 (vs 1992 in the other 5 species), and increased emphasis placed by observer

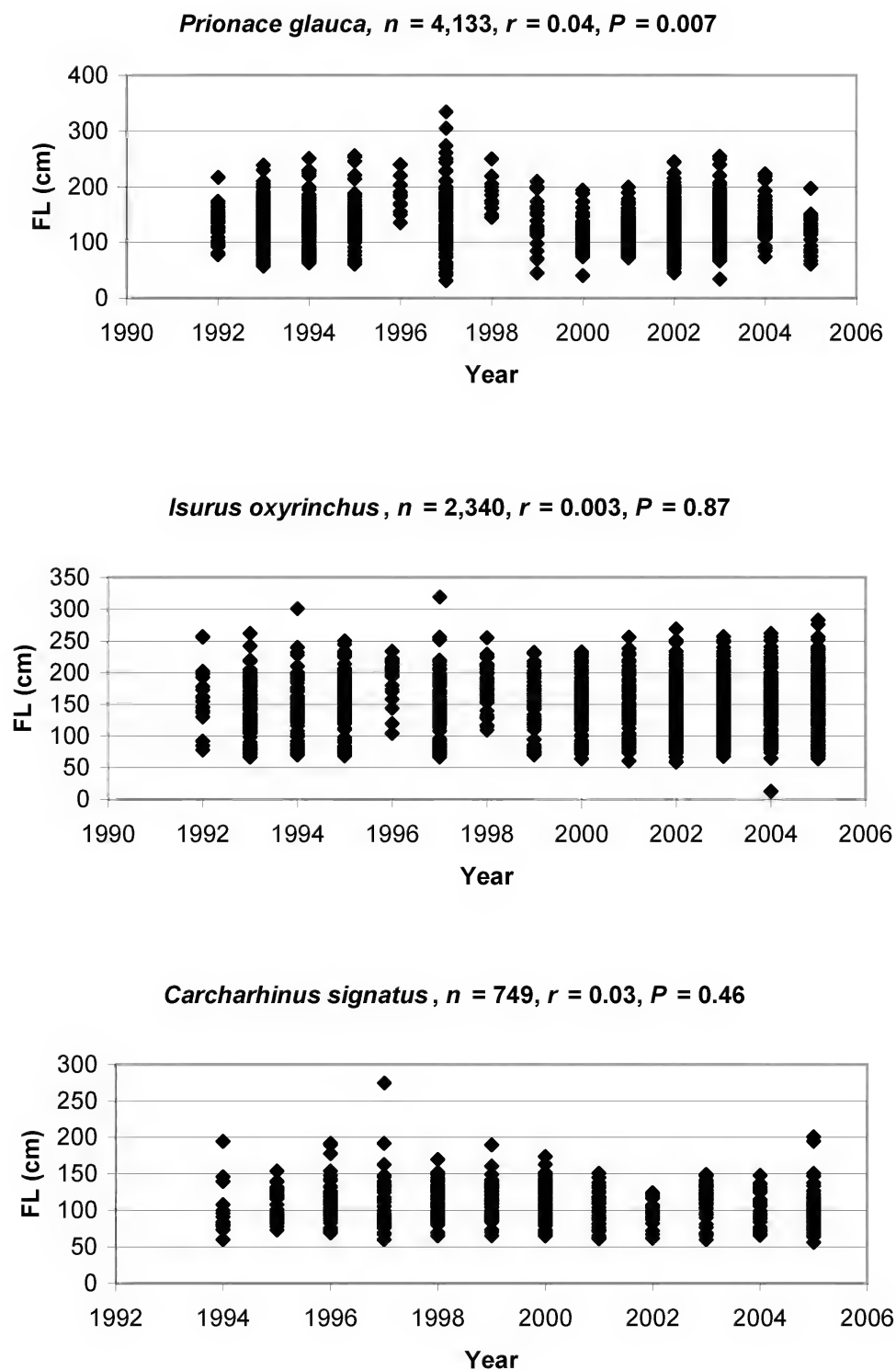


Figure 9. Observed fork lengths (FL) of blue, shortfin mako, and night sharks from the pelagic longline observer program. Fits of linear regressions to the data are indicated.

TABLE 2

Percent change in relative abundance (from beginning to end of the time series considered) for six shark species or genera reported in the present and two other studies. Logbook G+C is the logbook analysis restricted to the Gulf and Caribbean areas. Baum et al. (2003) used the logbook dataset (as in the present study); Baum and Myers (2004) compared surveys from the 1950s to observer data for 1995–1999. Periods covered are as follows: logbook (1986–2005), observer (1992–2005), logbook G+C (1986–2005), Baum et al. (2003) (1986–2000). ¹Numbers in parentheses refer to the decline in relative abundance during the same period covered by the observer dataset; ²Denotes that logbook data start in 1992, not 1986; ³Denotes that observer data start in 1994, not 1992.

Species	Logbook ¹		Observer		Logbook (G+C)		Baum et	Baum and
	Standardized	Nominal	Standardized	Nominal	Standardized	Nominal	al. (2003)	Myers (2004)
<i>Prionace glauca</i>	–88 (–73)	–50	–52	–43	–91	–90	–60	n/a
<i>Isurus</i> spp.	–43 (–25)	–36	–15	–34	–57	–63	–30	–45
<i>Alopias</i> spp.	–63 (–50)	–46	28	–39	–59	–63	–80	n/a
<i>Carcharhinus falciformis</i> ²	–50	38	–46	–40	–48	–51	n/a	–91
<i>Carcharhinus longimanus</i> ²	–57	–59	–9	–36	–75	–66	–70	–99
<i>Carcharhinus signatus</i> ^{2,3}	–50 (–29)	–29	192	14	–90	–63	n/a	n/a

staff on the verification of identifications of carcharhinid sharks beginning around 1998. In general, sample sizes for oceanic whitetip, thresher, and night sharks in the observer analysis were substantially lower than those for the other 3 species or genera, and thus the trends estimated should be regarded with caution. Conversely, misreporting and species misidentification are likely to be much more prevalent in logbooks. Burgess et al. (2005a) reported that Vietnamese-American longline fishers may sometimes call shortfin makos, “blue sharks” and that any large, brown-colored shark is generally called a “tiger shark.” Burgess et al. (2005a) also stated that changes in reporting practices may have accounted in part for the declines in relative abundance of multiple shark species in the Northwest Atlantic Ocean reported by Baum et al. (2003). Before implementation of the first US Atlantic Shark Management Plan in 1993 (NMFS 1993), all fishers targeting sharks, swordfish or tunas reported shark landings in the pelagic longline logbook from which data were used in Baum et al. (2003) and the present analysis. However, after implementation of the management plan, fishers could temporarily report to a new logbook program designed for fishers targeting sharks from 1993 to 1995. After 1995, fishers again had the option to continue reporting to the pelagic longline program or to a coastal fisheries logbook program that also includes longline gear. Another potential change in reporting practices is a tendency to under-report bycatch over time as fishers develop a growing perception that those reports result in increasingly restrictive management regimes. These various changes in logbooks and

potentially in reporting practices may have affected both Baum et al.’s (2003) and our analyses.

Additional factors that may have affected the analyses are changes in both hook size and type, not reported in the logbooks, and fishing depth related to the tuna species targeted. While we accounted for fishers switching between swordfish and tunas as target species, we did not account for the different depths at which gear is set when they target bigeye vs yellowfin tuna for example.

Comparison of the relative declines reported by Baum et al. (2003) and the present study revealed good agreement between the 2 studies (Table 2) as one would expect from analyzing the same dataset covering similar periods. This is true even though the statistical procedures (i.e., GLM) and factors considered differed between studies. We also found relative declines in our analysis of the logbook dataset restricted to the Gulf and Caribbean region, although not as accentuated as those reported by Baum and Myers (2004) for the silky and oceanic whitetip sharks in the GOM exclusively. Our analysis and that of Baum and Myers’ (2004), however, had little temporal overlap (Table 2).

In all, there is little doubt that populations of pelagic and other large-bodied shark species have decreased with respect to unexploited levels in the western North Atlantic Ocean and likely in other bodies of water. While the logbook dataset is the largest available for the western North Atlantic Ocean and the observer dataset is generally more reliable, the numerous caveats identified above and elsewhere by other authors dictate caution in interpreting

results. However, there is still some cause for optimism based on the recent trends obtained from both these datasets. Relative abundance of mako, thresher, silky, and night sharks in the western North Atlantic Ocean appears to have stabilized or even be increasing in some cases since the late 1990s, and relative abundance of oceanic whitetip sharks is also stable or increasing since 2000. Similarly, based on the logbook dataset, relative abundance of mako, thresher, night and oceanic whitetip sharks in the GOM and CAR seems to have stabilized since the late 1990s, and relative abundance of silky sharks to be increasing in the area since 2000.

Given the highly migratory nature of many of these pelagic species, catch rates derived from other parts of the Atlantic Ocean should also be examined, and in particular catch rates derived from long-term fishery-independent surveys should be carefully analyzed and continued to be monitored. Ultimately, conclusions about the status of pelagic shark stocks should not be based exclusively on the time series examined herein, but on a more comprehensive examination of trends throughout the range of these species and ideally in combination with information derived from stock assessments.

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Gregory L. Fulling
NOAA Fisheries

Dagmar Fertl
Geo-Marine, Inc.

Kevin Knight
Geo-Marine, Inc.

Wayne Hoggard
NOAA Fisheries

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DISTRIBUTION OF MOLIDAE IN THE NORTHERN GULF OF MEXICO

Gregory L. Fulling^{1,2}, Dagmar Fertl², Kevin Knight², and Wayne Hoggard¹

¹NOAA Fisheries, Southeast Fisheries Science Center, 3209 Fredric Street, Pascagoula, Mississippi 39567 USA

²Geo-Marine, Inc., 2201 K Avenue, Suite A2, Plano, Texas 75074 USA, E-mail gfulling@geo-marine.com

ABSTRACT We compiled all available sighting, stranding and bycatch data for the Family Molidae (molas) in the northern Gulf of Mexico (NGOM) to assess spatial and temporal distribution. Overall, 483 records were collected from shipboard and aerial surveys, fisheries bycatch, and strandings. Molas were recorded year-round, with a ubiquitous distribution in both nearshore and offshore waters. Ocean sunfish (*Mola mola*) were sighted with greatest frequency during the winter (December thru April) in sea surface temperature <24° C. Potential reasons for increased sightings during winter may be related to the lack of a well-defined thermocline in the NGOM; the species' "basking" behavior associated with thermoregulation; and oxygen replenishment after long, deep dives to oxygen-deficient depths.

RESUMEN Para determinar la distribución espacio temporal de la familia Molidae (molas) en la parte norte del Golfo de México (NGOM) se realizó una compilación de todos los datos de avistamientos (desde embarcaciones y censos aéreos), capturas pesqueras y varamientos disponibles. En total 483 registros fueron colectados. Los molas fueron registrados a lo largo de todo el año con una distribución universal en aguas tanto costeras como oceánicas. El pez sol (*Mola mola*) fue avistado con mayor frecuencia durante el invierno (de Diciembre a Abril) en donde la temperatura superficial del mar fue menor a 24° C. Una de las posibles razones del incremento de avistamientos durante el invierno puede estar relacionada a la bien definida termoclina en la NGOM; la especie muestra un comportamiento de reposo ("basking") asociado a la termorregulación y reabastecimiento de oxígeno después de un buceo prolongado en aguas profundas con deficiencia de oxígeno.

INTRODUCTION

Members of the Family Molidae (molas) are a poorly understood, highly derived group of fishes. This family is composed of four species—the slender mola (*Ranzania laevis*), sharptail mola (*Masturus lanceolata*), ocean sunfish (*Mola mola*), and southern ocean sunfish (*Mola ramsayi*). Recent genetic analysis confirms that there are two species within the genus *Mola*, with *Mola ramsayi* being limited to the southern hemisphere (Bass et al. 2005). The ocean sunfish is the most frequently encountered mola species, and it is considered sympatric with the sharptail mola (Santini and Tyler 2002).

Molas are found worldwide in tropical to temperate seas (e.g., Parenti 2003, Houghton et al. 2006). Despite their widespread distribution, little is known of the ecology, habitat preferences, physiology and metabolism of molas. In fact, most ecological data for these fishes are collected opportunistically as anecdotal accounts, strandings, and incidental catches. Recent reports indicate that molas are deep divers, active swimmers, and a common component throughout the water column in areas where they occur (Harbison and Janssen 1987, Seitz et al. 2002, Cartamil and Lowe 2004). Furthermore, incidental catches in fisheries demonstrate that molas are major components of gillnet and driftnet fisheries (e.g., Silvani et al. 1999, Cartamil and Lowe 2004) and are often also caught on longlines (e.g., Seitz et al. 2002, Desjardin 2005, this paper).

Since molas are not commercially important species, there are limited resources available to exclusively study these fishes and any available data or observations must be fully utilized to establish baseline information on the ecology and habitat association of these fishes where they occur. One example is an anecdotal report of a sharptail mola struck by the Johnson Sea-link submersible at a depth of 670 m off Chubbs Cays in The Bahamas (Harbison and Janssen 1987). Another example is results from opportunistic tagging of a sharptail mola with a pop-up satellite tag (PSAT) while conducting pelagic longlining in the northern Gulf of Mexico NGOM (Seitz et al. 2002). Their study reported that the sharptail mola spent 92.5% of its time at depths between 5 and 200 m, < 3% of the time at depths shallower than 5 m, and ~86% of the time in water with sea surface temperature (SST) greater than 20° C. Finally, Cartamil and Lowe (2004) tracked eight ocean sunfish using acoustic tags over a 24 to 72 hr period off southern California. Their data showed that ocean sunfish are active swimmers, able to travel distances of ~ 26 km/d, reaching speeds of 3.2 km/hr when active, and diving deeper than 50 m. These are good examples of the types of studies that are paramount to understanding more about molas, and specifically, the ocean sunfish.

Currently, under mandate from the Marine Mammal Protection Act (MMPA), the National Marine Fisheries Service (NMFS) is required to conduct assessment surveys designed to estimate the abundance of cetacean (whale

and dolphin) stocks that reside in US waters. During these surveys, other “species of interest” (including molas) are commonly sighted and recorded. Our objective here was to document the distribution of molas in the NGOM. We used aerial and shipboard survey data, opportunistic sightings, incidental fisheries bycatch, stranding records, and published tagging data for molas to document the family’s distribution in the NGOM.

METHODS AND MATERIALS

Study area

The study area was defined as waters of the NGOM between the US-Mexico border and Key West, Florida, from the shoreline extending south to the outer limits of the Economic Exclusive Zone (EEZ) into waters seaward of the 3,000 m isobath (ca. 699,070 km²). Major features of the NGOM include the wide shelf (up to 200 km) off Florida, Texas, and Louisiana. The shelf is narrower off the Florida Panhandle near DeSoto Canyon, the Mississippi River Delta, and southern Texas. The continental slope is a steep escarpment from 1,000–2,000 m in the eastern NGOM. This area is also subject to the quasi-annual incursion of the Loop Current (Sturges and Evans 1983), which can extend north of Tampa Bay, Florida (~28°N). This incursion can create cyclonic and anti-cyclonic gyres that can extend onto the western Florida shelf (Paluszkiwicz et al. 1983), creating nutrient upwelling episodes along its edges.

Data types

All available sighting, stranding, and bycatch records for molas were compiled. Previously published records were reviewed and included here (e.g., Palmer 1936, Rivero 1936, Gunter 1941, Baughman 1950, Springer and Bullis 1956, Kemp 1957, Dawson 1965, Bright and Pequegnat 1974, Seitz et al. 2002).

NMFS-SEFSC longline fishery bycatch data

The NMFS deploys fishery observers to collect catch data from US commercial fishing and processing vessels. In 1992, the NMFS initiated scientific sampling of the US large pelagic fisheries swordfish/tuna longline fleet. Scientific observers are placed aboard vessels to report daily catch and effort information, as well as bycatch of non-target species (Beerkircher et al. 2002). Information for the Gulf of Mexico is collected by the Pelagic Observer Program located at the Southeast Fisheries Science Center (SEFSC) Miami Laboratory. We obtained Molidae information from 1992 through 2005.

TABLE 1

Summary of Molidae records, separated by record type, season and data source. The category ‘other’ refers to miscellaneous records including published and anecdotal accounts, a location point from tagging, and sightings not from marine mammal aerial and shipboard surveys. OS = ocean sunfish (*Mola mola*), SM = sharptail mola (*Masturus lanceolatus*), and UID mola = unidentified species of mola.

Source/Mola	F	Sp	Su	W	Total
Aerial					
OS	9	13	8	71	101
Shipboard					
OS	0	36	4	0	40
Bycatch					
OS	1	6	2	2	11
SM	6	16	10	13	45
UID mola	62	64	44	95	265
Stranding					
OS	0	0	0	2	2
SM	0	0	0	1	1
Other					
OS	0	3	5	4	12
SM	3	0	1	2	6
Totals	81	138	74	189	483

Aerial and shipboard survey data

Data collected during NMFS-SEFSC shipboard surveys were used to provide additional information on the distribution of molas. These surveys were conducted during the summers of 2001 and 2003, while the 1996, 1997, 1999, 2000, and 2004 surveys occurred during the spring (Table 1; Figure 1A). The 2001 survey covered shelf waters between the 10 and 500 m isobaths, while the 2003 and 2004 surveys focused on oceanic waters between the 200 m isobath and the EEZ. Detailed shipboard survey protocols can be found in Fulling et al. (2003), Mullin and Fulling (2004), and Mullin et al. (2004).

Three primary aerial surveys using line-transect methodologies (Buckland et al. 2001) were conducted by the NMFS-SEFSC; these were GulfCet I, GulfCet II, and the Gulf of Mexico (GOMEX) surveys. In 1992, the NMFS-SEFSC, in cooperation with the Minerals Management Service, initiated research to assess cetacean abundance/distribution in the NGOM; this program was known as the GulfCet Program. The GulfCet I aerial surveys were conducted quarterly during 1992–1994; the study area was bounded by the longitude of the Florida-Alabama border and the Texas-Mexico border, taking place between the

100 and 2,000 m isobaths (Hansen et al. 1996; Figure 1B). GulfCet II surveys were biannual surveys during 1996–1998 covering the shelf and offshore waters (out to the 2,000 m isobath) off Alabama and Florida (Mullin and Hoggard 2000; Figure 1B). The GOMEX aerial surveys conducted in 1992–1994 were fall surveys designed to provide information on bottlenose dolphin (*Tursiops truncatus*) abundance/distribution (Blaylock and Hoggard 1994). These surveys covered bays, sounds, estuaries and shelf waters out to the 200 m isobath. The GOMEX surveys only covered 1/3 of the NGOM each year; and therefore, did not cover the entire NGOM in one survey (Figure 1C). Aerial surveys during 1997–1998 were supplemented with an infrared temperature probe mounted on the aircraft, thereby allowing instantaneous SST for each sighting.

RESULTS

We collected 483 mola occurrence records for the NGOM (Table 1). These did not include 2 known underwater sightings off the Dry Tortugas—one made by the Deep Worker submersible at 500 m by Sylvia Earle or an ROV sighting made at 520 m (Oceansunfish.org 2006), since exact coordinates or time of year could not be obtained. Molasses (sharptail mola and ocean sunfish) were sighted in both nearshore, shallow waters and deep, offshore waters, with no obvious concentrations in any particular locations (Figure 2). Molasses were sighted year-round (Figures 3A–D). No records of slender mola occurrence were collected in the NGOM. The greatest number of records were pelagic longline bycatches ($n = 265$) and were of unidentified mola species. Molasses were sighted and caught with greatest frequency during the winter and spring ($n = 189$ and 138 , respectively; Figure 3A, B). There were 166 ocean sunfish records, 101 of these were sightings made during aerial surveys. Winter aerial surveys accounted for 70% of the total sightings of the ocean sunfish ($n = 71$) with the greatest concentration of ocean sunfish occurring off the Florida Panhandle near DeSoto Canyon (Figure 4). Sixty-one of the 101 ocean sunfish sightings were collected in conjunction with instantaneous SST. These values ranged from 13.8 – 29.3°C ($\bar{x} = 19.9^\circ\text{C}$, $s_x = 0.45$) and 96.8% ($n = 59/61$) of those sightings occurred in temperatures $< 25^\circ\text{C}$ ($\bar{x} = 19.5^\circ\text{C}$, $s_x = 0.40$; Figure 5).

DISCUSSION

It is evident from our findings that sharptail mola and ocean sunfish are widely distributed in NGOM and are found in shallow waters over the continental shelf, as well as deeper waters over the continental slope and abyssal

plain. Temporal and spatial aspects related to GOMEX aerial survey effort in waters over the West Florida Shelf might explain the lack of sightings in this area. There is one area with a complete lack of aerial survey effort on the West Florida Shelf (Figures 1C). The remainder of the West Florida Shelf was surveyed during the fall, when we did not observe ocean sunfish basking. West of the Mississippi River, the lack of records is again likely due to the timing of the GOMEX aerial surveys—fall (Figure 1C). It should be noted that the DeSoto Canyon region is one of the few areas in the NGOM that received year-round aerial survey effort (specifically, GOMEX and GulfCet II).

Bycatch records and shipboard survey data proved invaluable for documenting the occurrence of these fishes, since these data addressed deeper waters (out to and seaward of the EEZ) that aerial surveys could not cover due to fuel/time constraints. Additionally, while not extensive with regards to coverage, fisheries bycatch data provided solid information on the distribution of molasses throughout the year. These data were independent of weather conditions that consistently affect sightability of the species with systematic surveys. Without these bycatch records, the interpretation of aerial survey data would have likely restricted the distribution of ocean sunfish in the NGOM to the DeSoto Canyon area during the winter when SST was lowest, as this is the region and season with the greatest number of aerial survey ocean sunfish sightings.

Several studies have demonstrated a relationship between cool water and mola sightings. For example, Lee (1986) sighted molasses with greatest frequency during cool water months (March–May, $n = 5/20$ sightings) in shallow waters off of North Carolina. Sims and Southall (2002) reported that nearly all of their ocean sunfish sightings occurred between 13° and 17°C in the English Channel, UK. Cartamil and Lowe (2004) found that acoustically tagged ocean sunfish encountered water temperatures ranging from 6.8 to 21°C off Southern California. Our study supports these findings, given that the mean SST for ocean sunfish sightings from our aerial surveys was $\sim 19.9^\circ\text{C}$. However, both of the studies mentioned occurred in areas where the water temperature is consistently cooler year-round than the waters in NGOM and during seasons when our sighting frequencies were the lowest (summer). Within the NGOM, Seitz et al. (2002) reported that a PSAT-tagged sharptail mola spent $\sim 86\%$ of the time in waters with temperatures $> 20^\circ\text{C}$, was located rarely above 5 m depth, and made dives to ~ 700 m experiencing water temperatures as low as 7°C . The animal tagged by Seitz et al. (2002), however, was caught on a longline with a hook set at 85 m in April and SST was 23.9°C . While water temperature preferences of the ocean sunfish are basin-specific, it is

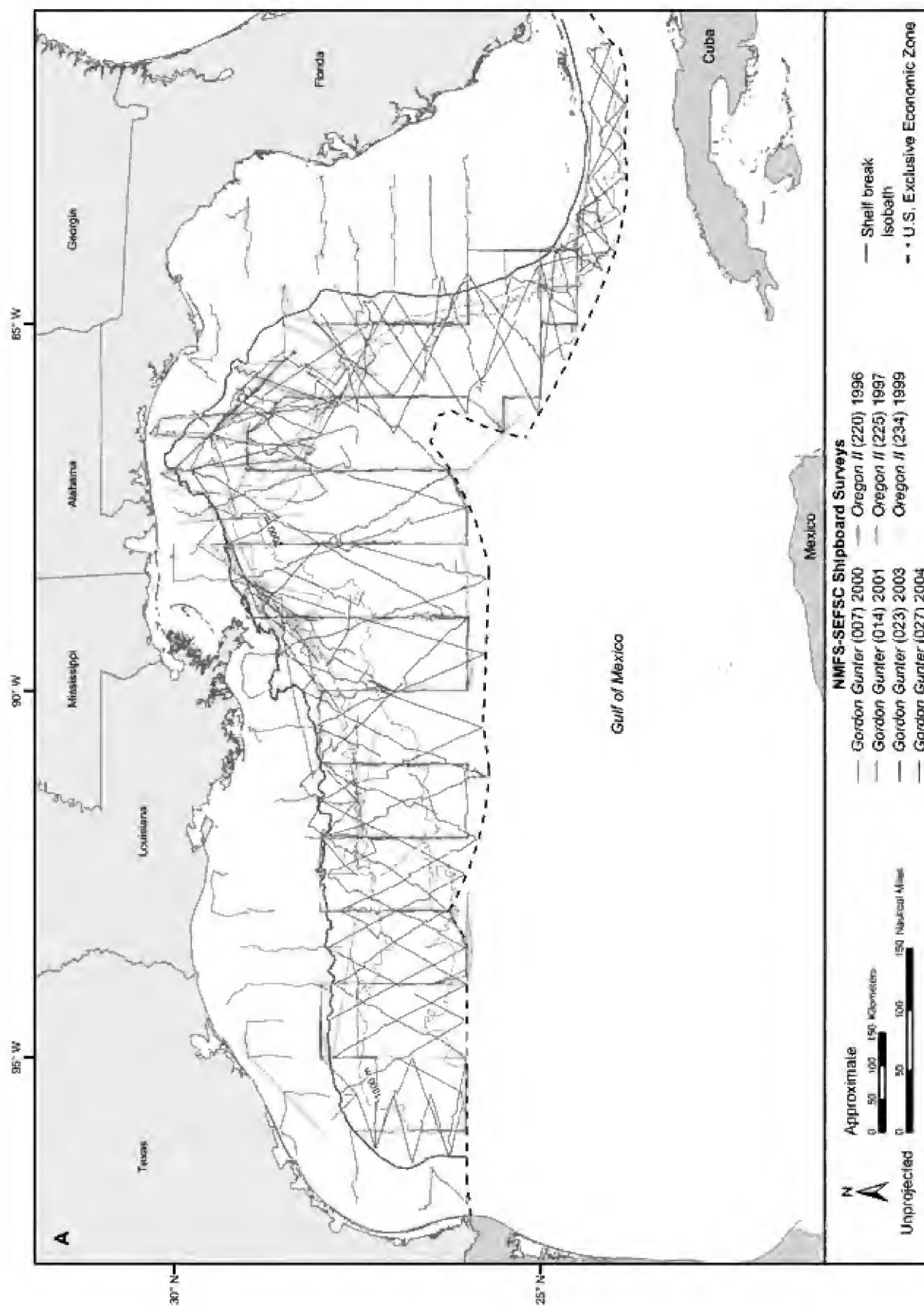
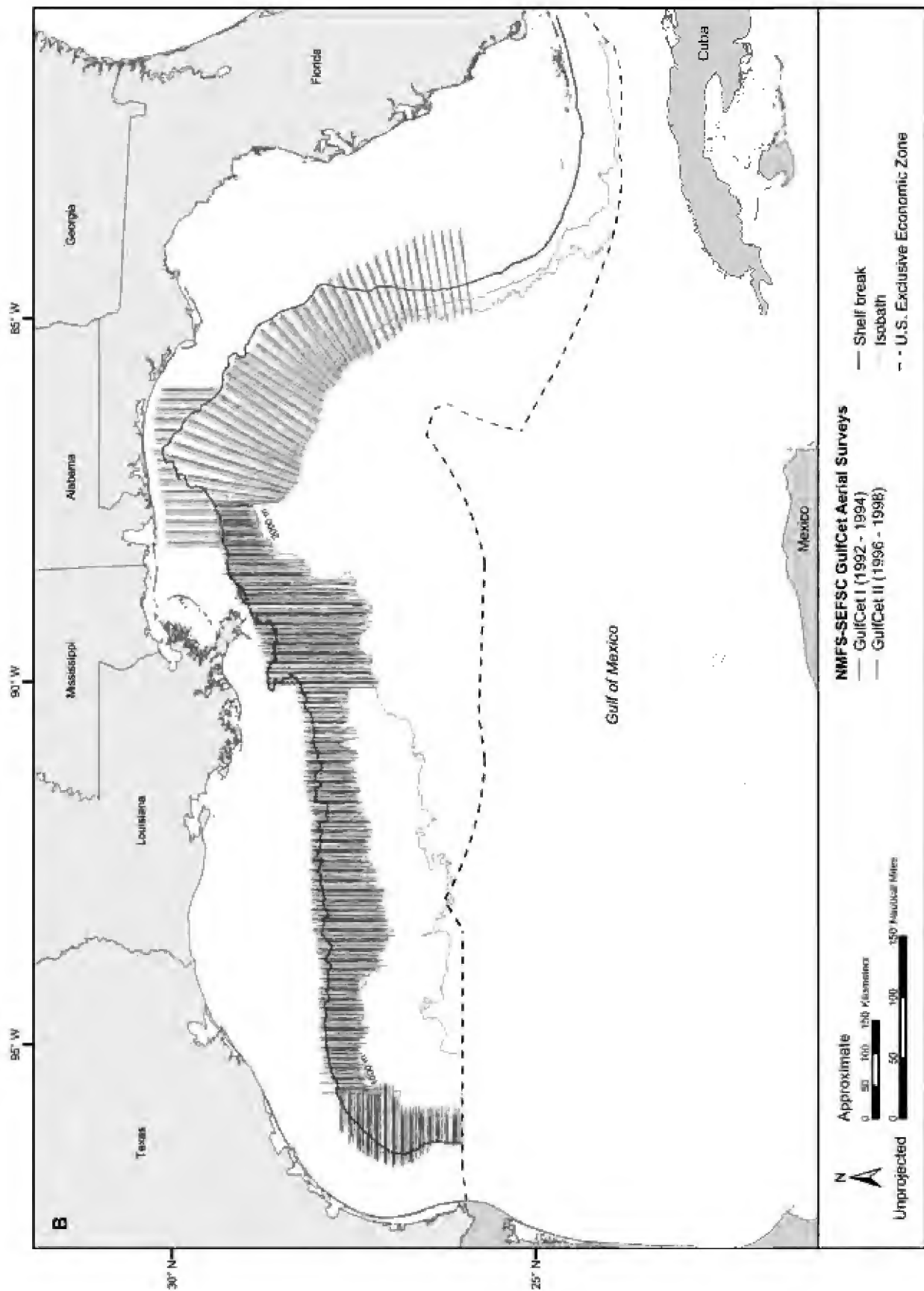
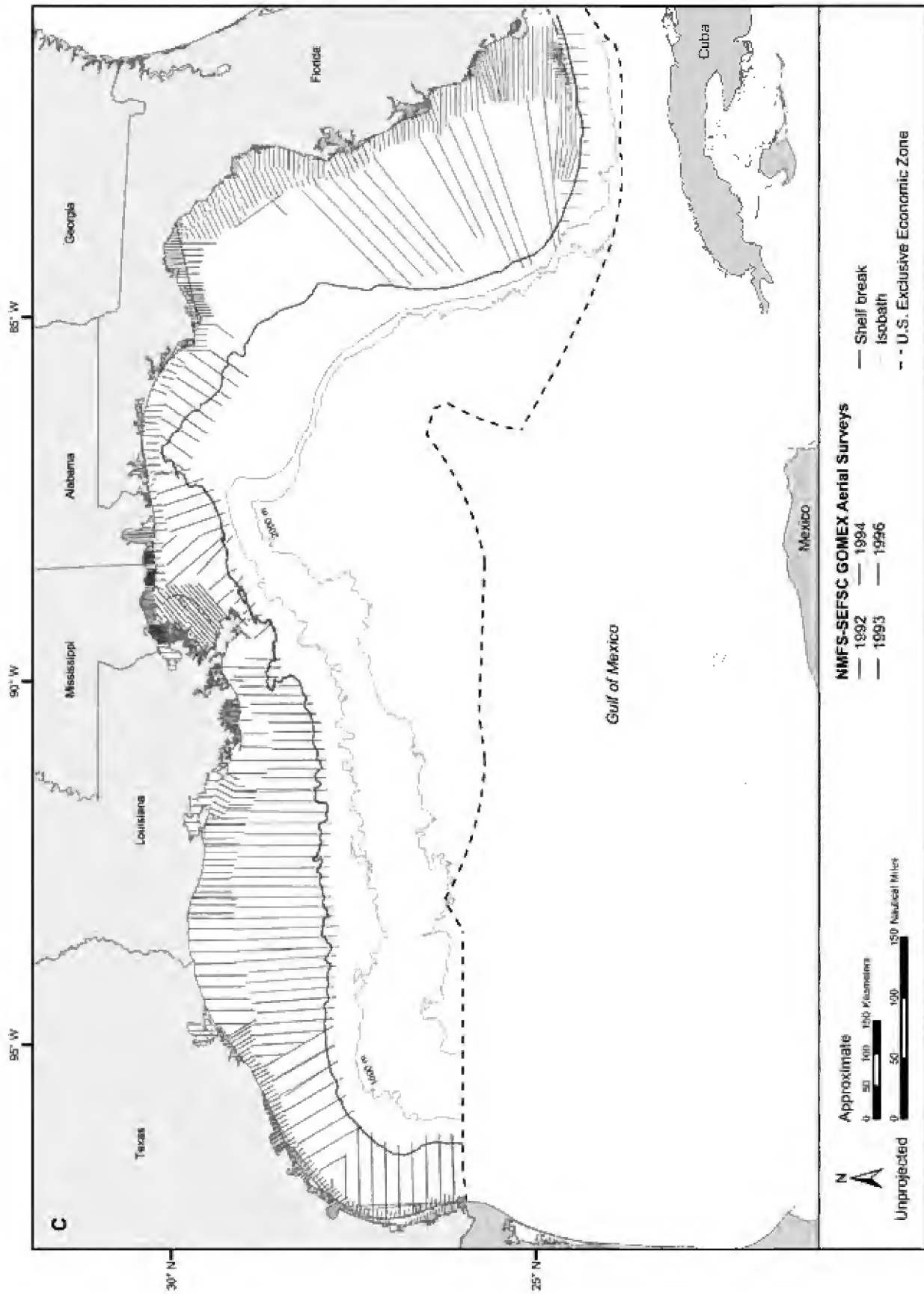


Figure 1. Survey effort from shipboard (A), and aerial surveys [GulfCet I and II (B); and GOMEX (C)] in the northern Gulf of Mexico. Shelf break, isobaths (1000 m increments), and Economic Exclusive Zone are depicted.





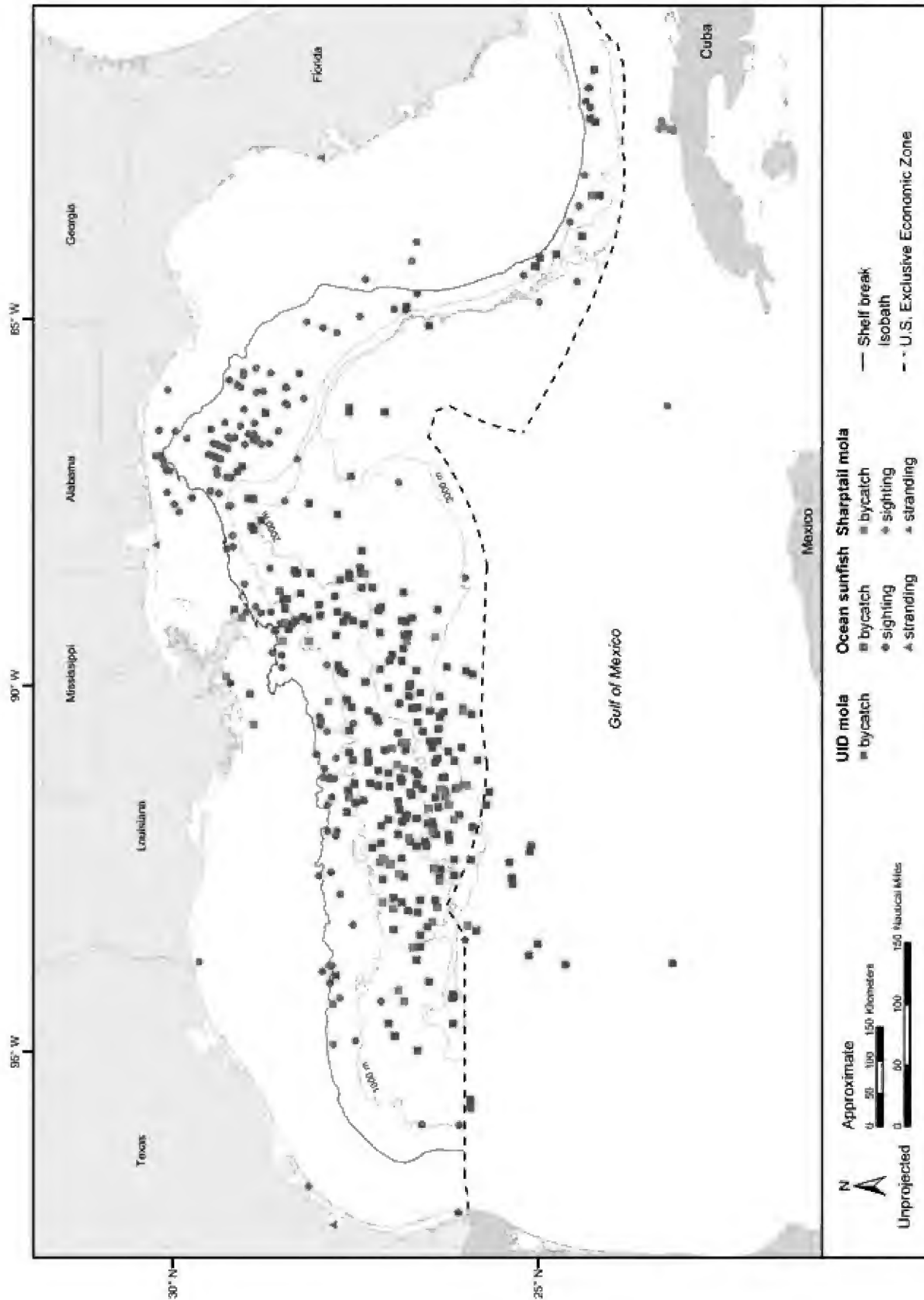


Figure 2. Distribution of Molidae from shipboard and aerial surveys, longline fisheries bycatch, strandings, published records, and anecdotal accounts. Shelf break, isobaths (1000 m increments), and Economic Exclusive Zone are depicted.

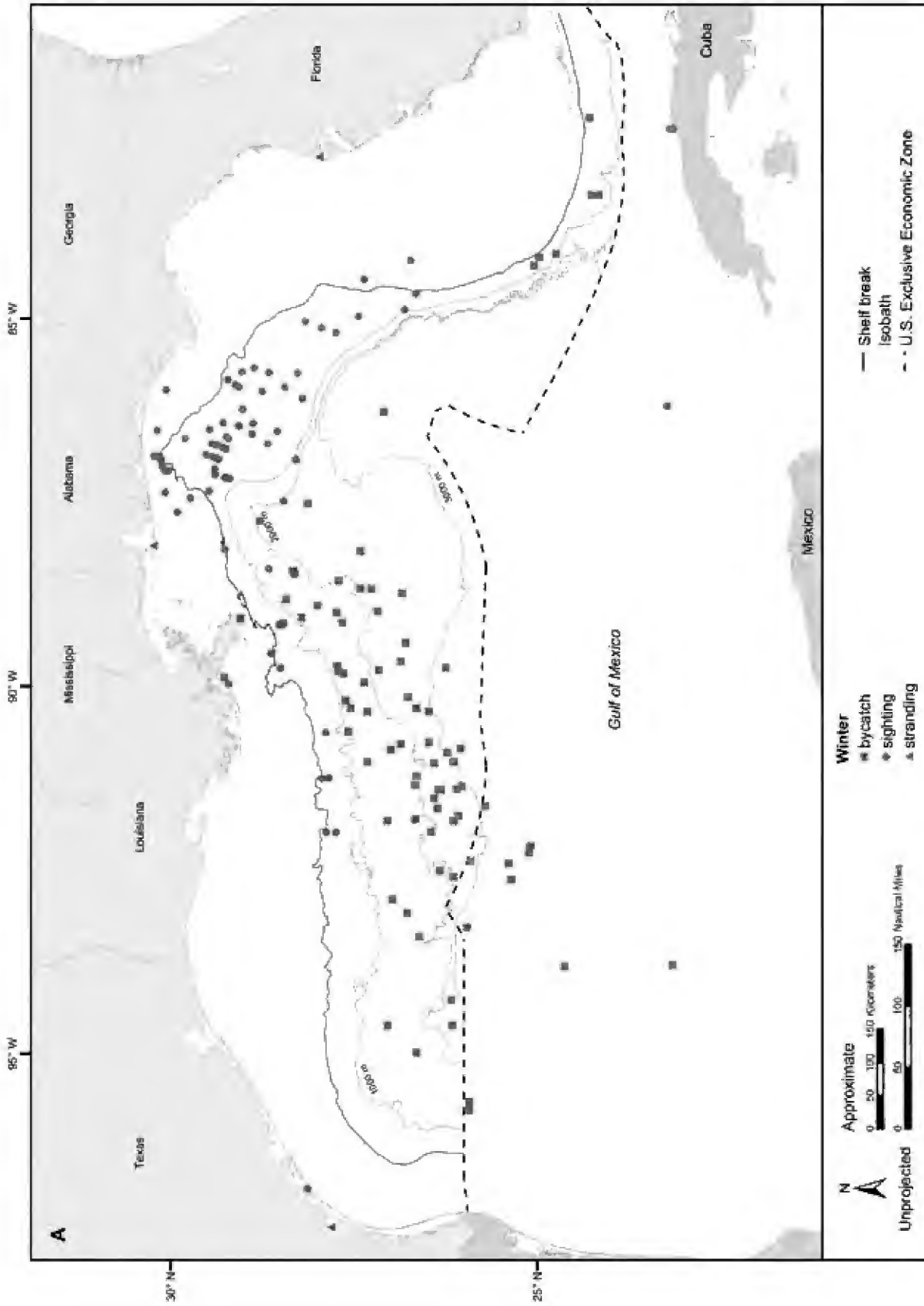
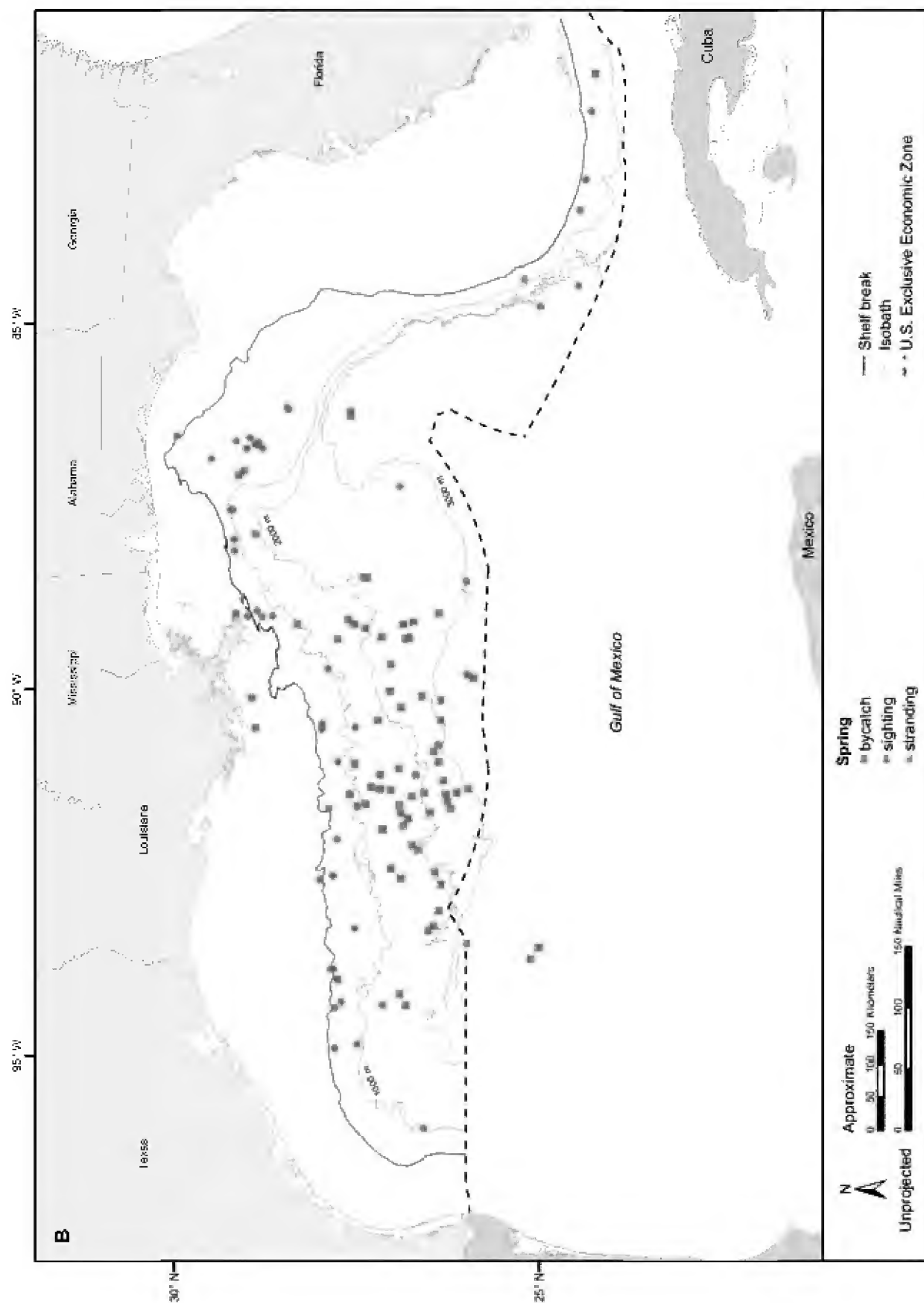
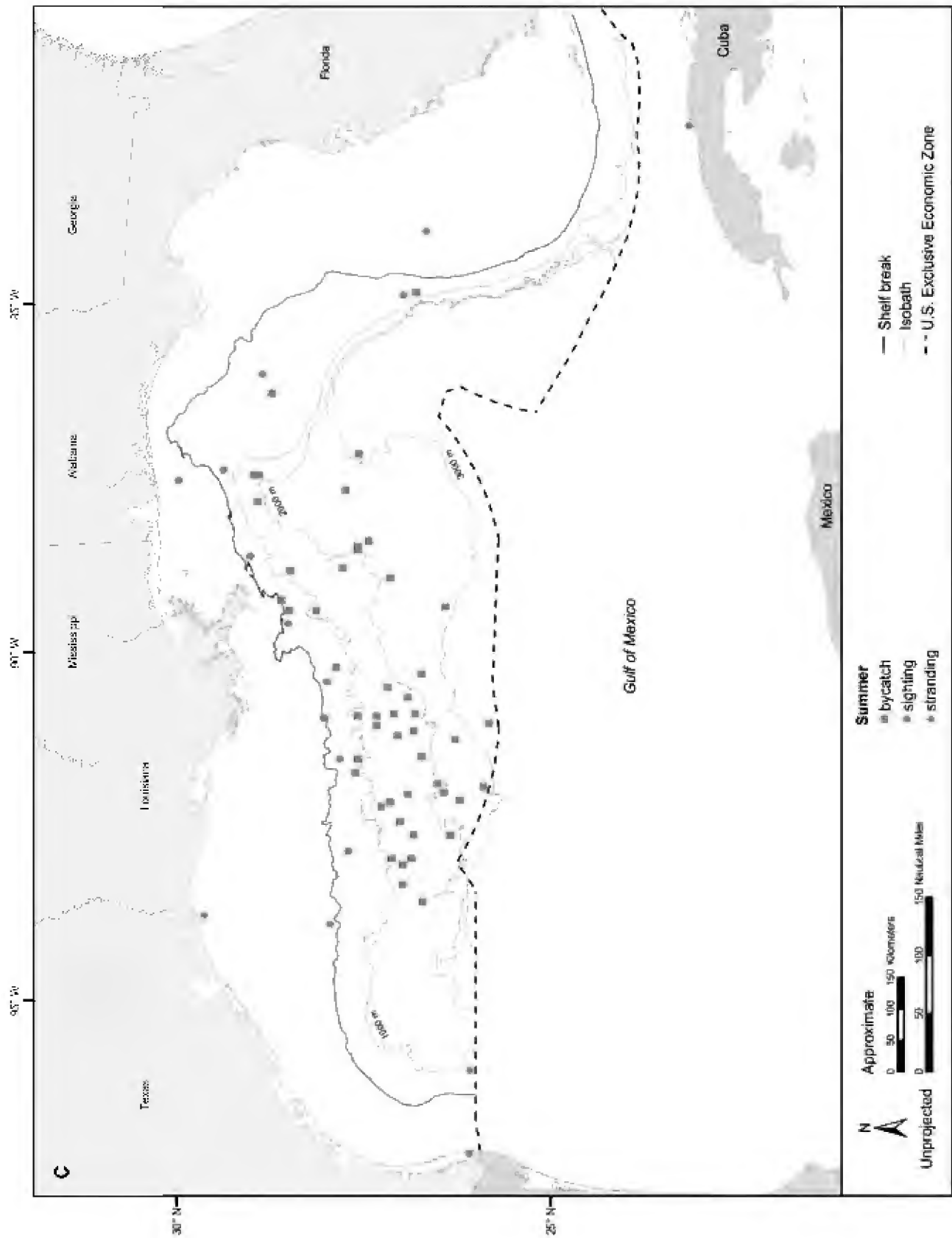
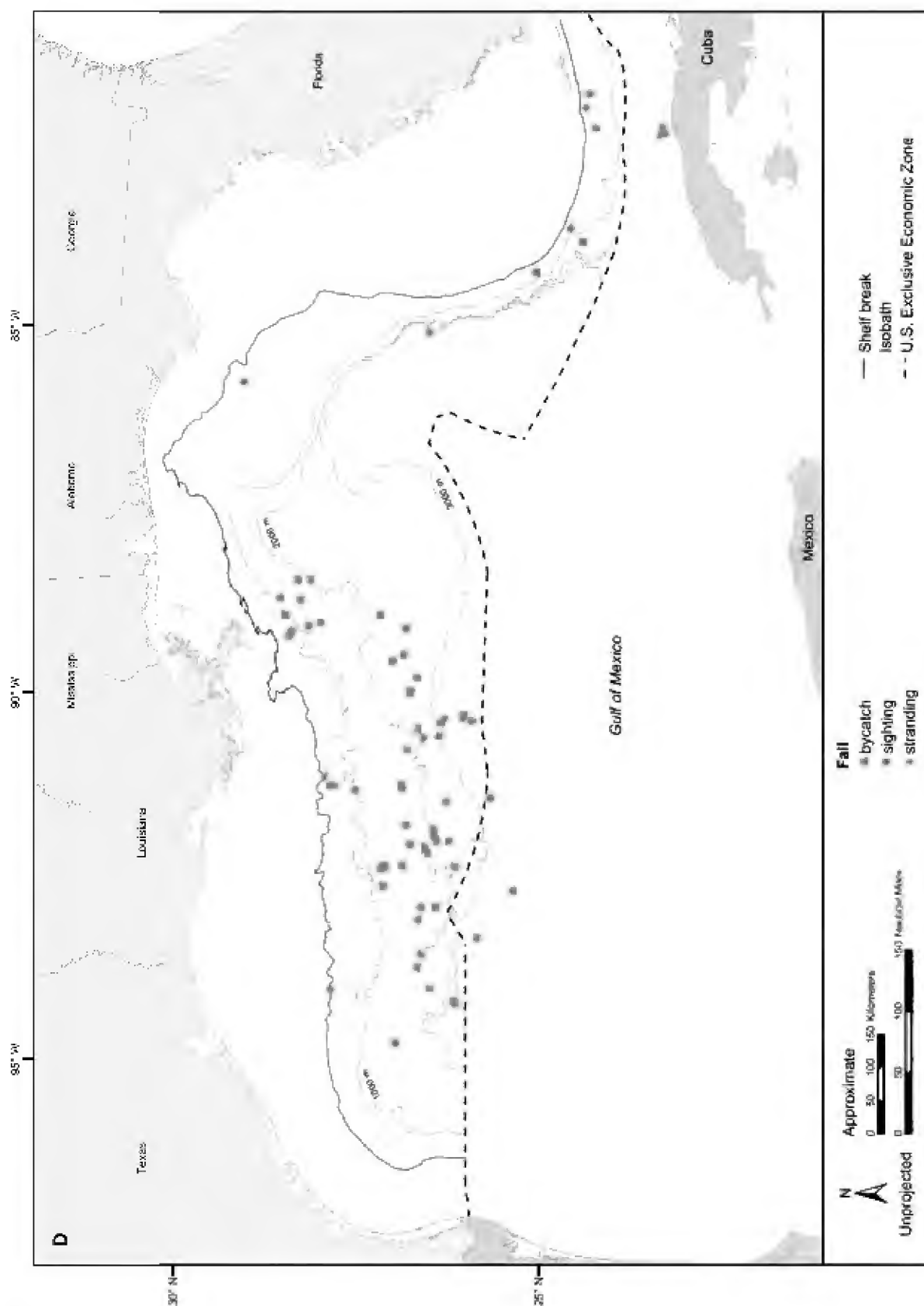


Figure 3. Seasonal break downs of Molidae from shipboard and aerial surveys, fisheries bycatch, strandings, published records, and anecdotal accounts. Winter (A), Spring (B), Summer (C), and Fall (D). Shelf break, isobaths (1000 m increments), and Economic Exclusive Zone are depicted.





MOLIDAE IN NORTHERN GOM



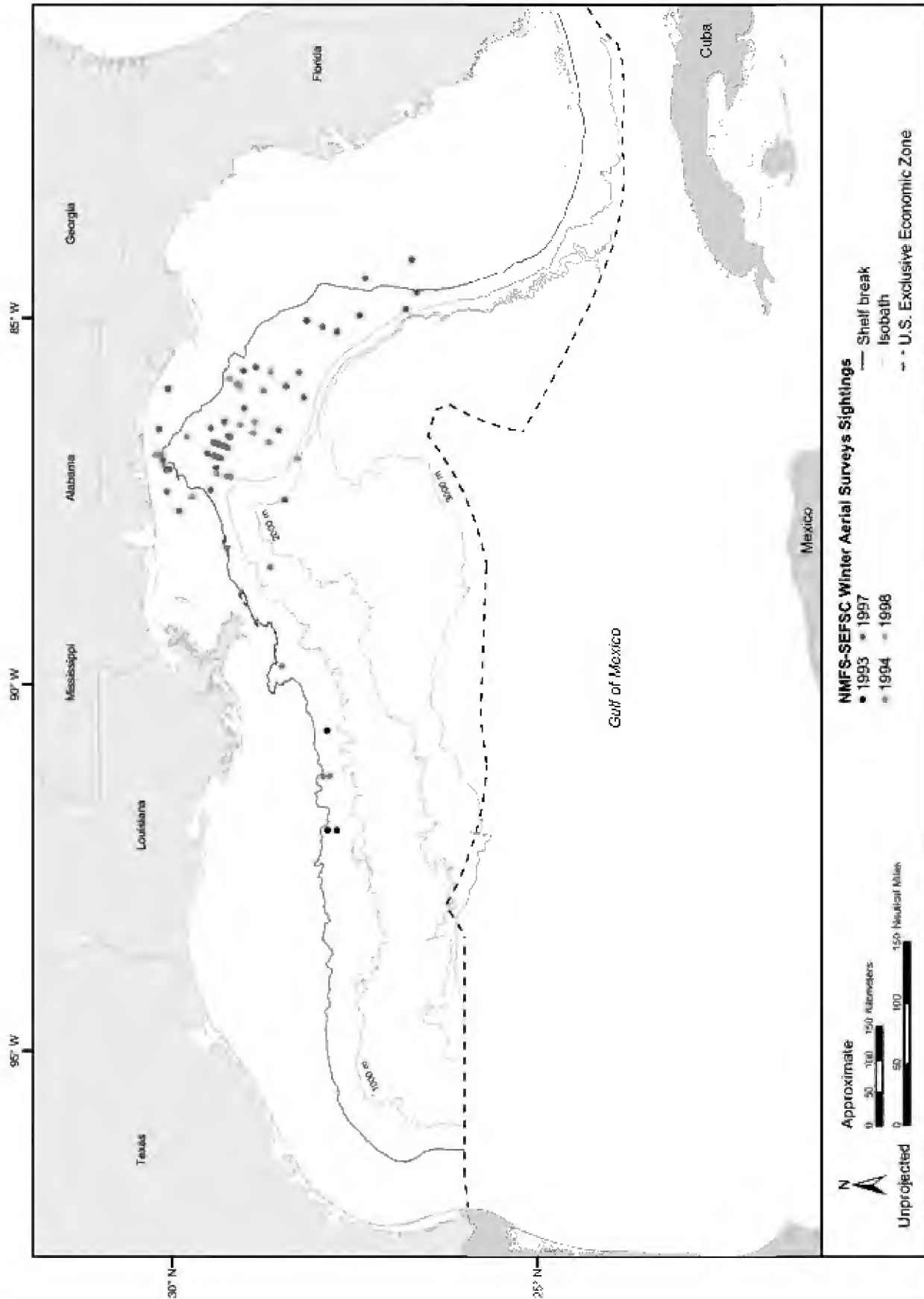


Figure 4. All ocean sunfish (*Mola mola*) sightings from winter aerial surveys. Shelf break, isobaths (1000 m increments), and Economic Exclusive Zone are depicted.

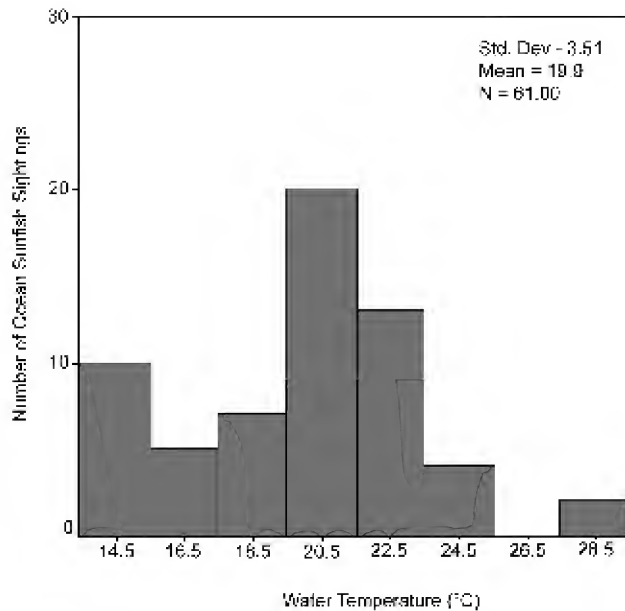


Figure 5. Ocean sunfish (*Mola mola*) sightings relative to sea surface temperature (°C) from 1997 and 1998 NMFS-SEFSC aerial surveys.

evident that water temperature in combination with thermocline depth may be important drivers in the distribution of ocean sunfish.

The majority of records (other than bycatch and strandings) we collected were of molas “basking” at the surface. This behavior is not well understood and has been suggested by some to only be exhibited by those molas which are sick and near death (Fraser-Brunner 1951, Schwartz and Lindquist 1987). This thought no longer appears valid given the accounts of mola sightings, tagging studies and the ability of those tagged animals to consistently be tracked for long periods of time after capture (T. Thys, per. comm., Sea Studios Foundation, Monterey, CA). Molas are consistently shown to frequent cold, deep waters (Harbison and Janssen 1987, Seitz et al. 2002, Sims and Southall 2002, Cartamil and Lowe 2004) on what are likely feeding dives, based on underwater sightings from semi-submersibles where high concentrations of their gelatinous prey also have been simultaneously observed (Harbison and Janssen 1987). Cartamil and Lowe (2004) also found that ocean sunfish spend a significant amount of time within the warmer near surface waters following these deep dives to cooler waters. Ascents to the warmer surface waters to increase body core temperature may be a mechanism for increasing metabolism (Cartamil and Lowe 2004). Within the NGOM, basking behavior may not take place year-round, since water temperatures increase during warmer months of the year and warmer waters are encountered deeper in the water column. Therefore, thermocline depth during other seasons may be an important

factor in low sighting rates in various regions including the NGOM.

Depth of the thermocline is area specific and variable depending on dominant currents. The thermocline is well developed and rarely absent off the California coast regardless of season. However, in the NGOM the thermocline is absent or very deep in the cooler months (> 100 m, November–April), while averaging ~ 40 m in the spring and summer (Weatherly 2004). The lack of a well-defined thermocline during winter months would require ocean sunfish to move into shallower waters to gain any thermal benefit. Variation in thermocline depth may explain the difference in the amount of time molas spend in the warmer mixed layer between the waters off California (Cartamil and Lowe 2004) and the NGOM (Seitz et al. 2002). Support for this concept comes from a recently PSAT-tagged ocean sunfish that swam from Massachusetts to the NGOM, north of the Yucatan Peninsula and equally distant from both Mexico and Cuba (I.F. Potter, per. comm., University of New Hampshire, Durham, NH). Dive records collected from that PSAT indicated the animal remained deeper in the water column the further south it traveled.

Additionally, deep dives by ocean sunfish for feeding subject these fish to water depths with low dissolved oxygen (DO) levels which may be considered stressful. As with swordfish (*Xiphias gladius*) (Carey and Robison 1981), ocean sunfish may be required to ascend to water depths high in DO to physiologically recover. This concept is supported by Cartamil and Lowe (2004) who showed that tagged fish spent a significant amount of time in the warm mixed layer after making long, deep dives off southern California. There are likely several benefits to basking behavior such as a combination of increasing body temperature and physiological recovery. Further behavioral and physiological studies are warranted.

One potential problem with these survey data is misidentification of the two mola species occurring in the NGOM (sharptail mola versus ocean sunfish). Since these data were not collected with molas as a focus, this concern cannot be addressed at this time. However, more recent surveys are now addressing this issue, with training of observers for species identification. The other concern is that the ocean sunfish could be mistaken for another fish, the opah or moonfish (*Lampris regius*). This possibility seems unlikely given the fact that the opah has a well-defined caudal peduncle and fin. It is therefore unlikely, that this species was confused with molas.

Ocean sunfish do not have to come to the surface to breathe, thus, animals below the surface were missed. Some sightings may have been detected, but were not recorded since observers were instructed to ignore other species

(including ocean sunfish) if they were interfering with detecting and recording the target species (i.e., marine mammals and sea turtles).

Concentrations of ocean sunfish near DeSoto Canyon from aerial surveys are interesting and may be unique given the location of these sightings. This region of the NGOM is influenced by incursions from the Loop Current and the Mississippi River plume. Both of these oceanic features are known to greatly enhance primary productivity (Lee et al. 1992, Lohrenz et al. 1999, Wiseman and Sturges 1999), thereby creating highly productive regions for higher trophic levels (Biggs and Ressler 2001). Further work in this region is needed and may provide further information on the habitat requirements of the two mola species known to occur in the NGOM.

In summary, for the NGOM, winter aerial surveys are most productive for generating sightings of molas. In fact, recent surveys for cetaceans off the US Atlantic coast (between Cape Hatteras, North Carolina and Savannah, Georgia) demonstrated that ocean sunfish were spotted with higher frequency in the winter instead of the summer months (G. Fulling and W. Hoggard, per. observ.). More specifically, aerial surveys are more beneficial for sighting molas than shipboard surveys since the altitude and speed of the platform allows for greater frequency and probability of detection. However, the high costs associated with aerial surveys likely preclude these platforms as regular survey mechanisms for dedicated mola studies, particularly since molas are not of commercial interest and as a result there are no management implications for them. It is therefore imperative to collect these data in conjunction with other dedicated surveys on a "non-interference" basis.

Further attempts to collect data will build on the information presented here and will enhance our understanding of these unique fish. Future work must incorporate PSATs which have been and will continue to be very useful in providing valuable information to address many unknown aspects of molas. These types of studies are currently ongoing in the North Pacific, conducted by the Monterey Bay Aquarium (T. Thys, per. comm., Sea Studios Foundation, Monterey, CA). More detailed analyses of fisheries bycatch (both longline and trawl) data will also be critical in our understanding of distributional and behavioral ecology of both mola species common to the NGOM. Though our study was restricted to readily available data from other sources, we have demonstrated that there is a need to incorporate all sources of information to elicit more knowledge on the ecology of a relatively unknown species.

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Observations of a Feeding Aggregation of Whale Sharks, *Rhincodon typus*, in the North Central Gulf of Mexico

Eric R. Hoffmayer

University of Southern Mississippi

James S. Franks

University of Southern Mississippi, jim.franks@usm.edu

William B. Driggers III

National Marine Fisheries Service

Kenneth J. Oswald

University of South Carolina

Joseph M. Quattro

University of South Carolina

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OBSERVATIONS OF A FEEDING AGGREGATION OF WHALE SHARKS, *RHINCODON TYPUS*, IN THE NORTH CENTRAL GULF OF MEXICO

Eric R. Hoffmayer^{1*}, James S. Franks¹, William B. Driggers III², Kenneth J. Oswald³, and Joseph M. Quattro³

¹Center for Fisheries Research and Development, Gulf Coast Research Laboratory, The University of Southern Mississippi, 703 East Beach Drive, Ocean Springs, Mississippi 39564 USA, *E-mail eric.hoffmayer@usm.edu

²National Marine Fisheries Service, Southeast Fisheries Science Center, Mississippi Laboratories, PO Drawer 1207, Pascagoula, MS 39567 USA

³Department of Biological Sciences, University of South Carolina, Columbia, South Carolina, 29208 USA

ABSTRACT On 26 June 2006 an aggregation of 16 whale sharks was observed for a period of 4 hr in the north central Gulf of Mexico (GOM). The sharks remained within an area about 1.0 km² in size and continuously ram filter fed at the surface. Visual analysis of a plankton sample collected from the study site revealed the presence of copious amounts of fish eggs in mid-embryonic development and a minor amount of other zooplankton. A second plankton sample (control) collected about 3.5 km from the study site in an area where no whale sharks were present contained few eggs, however other zooplankton were similar to the study site sample in species composition and abundance. Two egg morphs were identified, and samples of one of the morphs, which represented 98% of the eggs at the study site, were verified by genetic analysis as little tunny, *Euthynnus alletteratus*. The observed feeding behavior and the abundance of fish eggs at the study site indicated the whale sharks were feeding on recently spawned little tunny eggs. This represents the first confirmed observation of a feeding aggregation of whale sharks in the GOM.

RESUMEN El 26 de Junio del 2006 un agrupamiento de 16 tiburones ballena fue observado por un periodo de 4 horas en el centro norte del Golfo de Méjico (GOM). Los tiburones permanecieron dentro de un área alrededor de 1.0 km² y continuamente se desplazaron filtrando alimento en la superficie. Un análisis visual de una muestra de plankton colectada en el sitio de estudio revela la presencia de grandes cantidades de huevos de peces en un desarrollo intermedio del embrión y una pequeña cantidad de otro zooplancton. En un área donde no habían tiburones ballena, una segunda muestra de plankton (control) colectada (alrededor de 3.5 km. del sitio de estudio) presento pocos huevos de peces, sin embargo el otro zooplancton fue similar en composición de especies y abundancia con la muestra colectada en el sitio de estudio. Dos formas de huevos fueron identificadas, la forma que represento el 98% de los huevos en el sitio de estudio fue identificada mediante un análisis genético como bacoreta, *Euthynnus alletteratus*. El comportamiento de alimentación observado y la abundancia de huevos de peces en el área de estudio indicaron que los tiburones ballena se alimentaron de un desove de huevos reciente de bacoreta. Esto representa la primera observación confirmada de una agregación de tiburones ballena en el GOM.

INTRODUCTION

The whale shark, *Rhincodon typus* (Smith 1828), is the largest fish in the sea, is distributed circumglobally in tropical and subtropical marine waters except for the Mediterranean Sea (Compagno 2001), and is threatened (Stewart and Wilson 2005). Despite their large size and ubiquitous distribution, little is known about their biology and behavior. They are opportunistic filter feeders (Taylor et al. 1983, Colman 1997) that aggregate in areas of high localized productivity, e.g., mass spawning events identified near Ningaloo Reef, Australia (Colman 1997, Wilson et al. 2001), La Paz, Mexico (Clark and Nelson 1997), and Gladden Spit, Belize (Heyman et al. 2001).

Whale sharks were first reported in the Gulf of Mexico (GOM) by Gudger (1939), with subsequent sightings of solitary individuals off Texas (Baughman 1947, Gunter and Knapp 1951, Hoffman et al. 1981), Mississippi

(Springer 1957), and Florida (Clark and von Schmidt 1965). Also, the presence of whale shark aggregations in the region have been noted (Gudger, 1939, Hoffmayer et al. 2005, Burks et al. 2006), and these authors suggested that the aggregations occurred in response to feeding opportunities. We report on an opportunistic encounter with an aggregation of 16 whale sharks on 26 June 2006 in the GOM west of the Mississippi River Delta (Delta).

MATERIALS AND METHODS

An on-site investigation was conducted on 26 June 2006 to confirm recent reports by mariners of whale sharks aggregating in the north central GOM in the vicinity of the Delta. With a spotter aircraft searching a 129 km² area off the Delta, an aggregation of whale sharks was located ~70 km southwest of the mouth of the Mississippi River

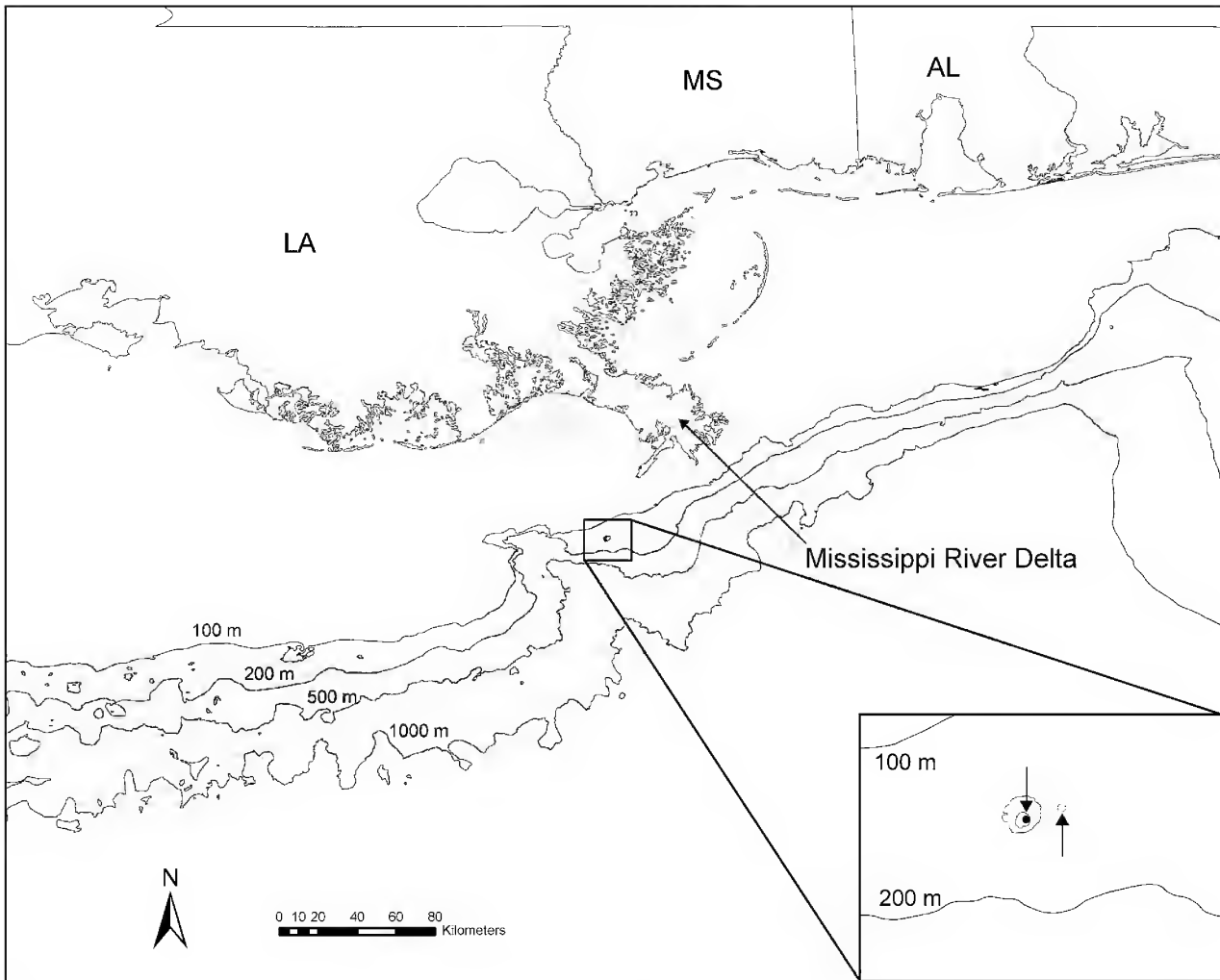


Figure 1. Map of the north central Gulf of Mexico showing the location of the study (closed circle) and control sites (open circle) (see inset). The study site was located in surface waters 78 meters (m) above the eastern edge of the crest of a topographic high, the base of which is located at 100 m water depth. Exact latitude and longitude of the study site can be obtained from the authors.

between 0800 to 1200 hr. The sharks remained in surface water within $\sim 1.0 \text{ km}^2$ area over the crest of a small-scale, shelf-edge topographic high (Rezak et al. 1983), henceforth referred to as the study site (Figure 1).

The total length (TL, m) of several sharks was estimated as they individually swam parallel with the 11 m vessel (Figure 2a). No gender data were recorded. Surface observations of the whale sharks' behavior were made visually from the vessel, and aspects of their behavior were documented with digital video and still photography. Surface water temperature ($^{\circ}\text{C}$), salinity (psu), and dissolved oxygen (mg/l) were recorded at the study site using a YSI meter (Model 85), and water depth (m) was recorded using a Furuno FE700 Echo Sounder. Surface plankton was collected at the study site using a 60 cm diameter plankton net (0.333 mm mesh) towed for 10 min (1040–1050 hr)

at a speed of 61.7 m/min. Following the same protocol, between 1325–1335 hr a second plankton sample (control) was collected 3.5 km east of the study site (Figure 1). Plankton samples were preserved in 95% ethanol and later examined in the laboratory. The volume of water filtered by the plankton net was calculated as $V = D \times A$, where V is the volume of the water filtered (m^3), D is the distance of the plankton tow (speed \times time, m), and A is the area of the plankton net mouth (m^2).

Plankton settled volume for the study and control sites were determined with a Motoda plankton splitter box by allowing a 1/16 split of the sample to settle into a 250 ml graduated cylinder for 24 hr. Egg counts were performed from a 1/256 split of the sample using an Olympus dissecting scope. The density of eggs for each tow was standardized to the number of eggs per m^3 of water filtered.

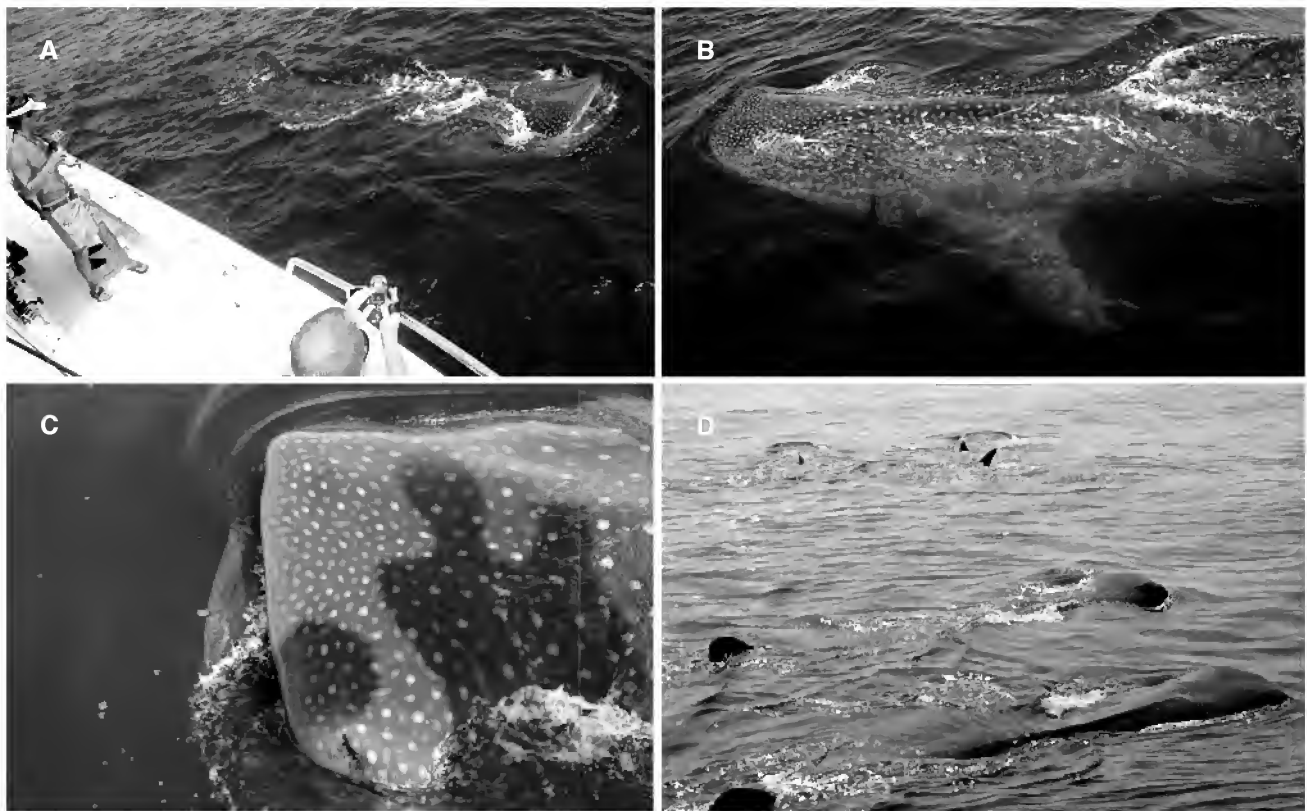


Figure 2. Images showing whale sharks, *Rhincodon typus*, feeding on 26 June 2006 in the north central Gulf of Mexico. A) Total lengths were estimated by aligning the 11 m vessel with the shark and estimating size. B) Whale shark swimming horizontally showing ram surface filter feeding. C) Close up of a whale shark mouth while surface ram filter feeding; upper jaw is above the water's surface while the lower jaw is submerged. D) An image of 2 whale sharks swimming adjacent and parallel in the foreground and background.

A subsample of the eggs was examined to determine size (diameter, mm) and developmental stage (Kendall et al. 1984) using an Olympus dissecting microscope equipped with a calibrated ocular micrometer. A gross microscopic survey of the zooplankton sample was performed to identify component species (Smith and Johnson 1996).

Eggs morphs (see below) were identified genetically via direct amplification and sequence analysis of the mitochondrial DNA 16S locus. Template DNA was isolated from individual eggs using GeneReleaser (BioVentures Inc.) following the manufacturers' protocol. An aliquot of this egg/GeneReleaser solution was used in a PCR reaction that amplified a portion of the mtDNA 16s rDNA using primers and conditions as described in Quattro et al. (2001). Purified amplification products were used as templates for ABI Big Dye Terminator cycle sequencing reactions. Fragments were analyzed on an Applied Biosystems 3730 automated DNA sequencer. Sequences were edited with SEQUENCHER (Gene Codes Corp.) and subjected to BLAST (Altschul et al. 1990) searches against the GenBank NR DNA database (Benson et al. 2005).

Finally, we observed schools of little tunny (*Euthynnus alletteratus*) and collected 2 specimens at the study site. Gonads were removed, preserved in 10% buffered formalin, and processed for histological examination, following standard histological procedures, to determine gonadal maturity. No fish were observed or caught at the control site.

RESULTS

The 16 whale sharks we observed were skimming the surface of the water as they swam with their lower jaw positioned slightly under the surface, an activity that was interspersed with periodic gulping and contraction of the buccal cavity which caused lateral displacement of the gill slits (Figures 2b, c). Additionally, "coughing" behavior was observed. Individual sharks swam continuously on a steady course at ~3.7 km/h for a few minutes and then changed course. Frequently, some of the sharks appeared to pair off and swim parallel and adjacent to each other (Figure 2d). The estimated lengths of the whale sharks ranged from 6.0 to 12.0 m TL, with most being >8.0 m TL.

Surface water quality conditions were typical of summer except depth was 78 m at the study site whereas it was 111.0 m at the control site. Each plankton net tow filtered ~174.4 m³ of surface water. Plankton settled volume was 5x higher in the study site sample (50 ml) than the control site sample (10 ml), with the primary difference being the high volume of eggs (40 ml) in the study site sample. The density of eggs was 106x higher in the study site sample (9,000 eggs m⁻³) than in the control sample (85 eggs m⁻³).

Eggs from the study site were in mid-embryonic developmental stage (Kendall et al. 1984) and were represented by 2 egg morphs. Morph 1 represented 98% of the eggs collected and ranged 0.70 to 0.80 mm in diameter with a single oil globule which ranged 0.16 to 0.20 mm in diameter. Morph 2 ranged 0.56 to 0.63 mm in diameter with a single oil globule that ranged 0.18 to 0.20 mm in diameter. Eggs identified from the study site sample were identical in appearance and size but not density to eggs collected at the control site. Sequence analysis and subsequent DNA database searches revealed high homology between 16S rDNA sequences from egg morph 1 and egg morph 2 and sequences from little tunny (*Euthynnus alletteratus*) and crevalle jack (*Caranx hippos*), respectively. Homology in each case was very high: 561 of 561 bases compared were identical between our egg morph 1 sequences and little tunny (GenBank accession AB099716), while 563 of 565 bases compared were identical between our egg morph 2 sequences and a crevalle jack sequence (GenBank accession DQ532847) deposited in GenBank.

Histological assessments of gonadal tissue collected from little tunny (1 male, 1 female) at the study site showed them to be in spawning condition. Ovarian tissue contained post-ovulatory follicles (POF), indicative of recent spawning (<24 hr) (Brown-Peterson et al. 2001), and testes contained sperm ducts filled with sperm.

There was no obvious difference in the species composition of zooplankton between the study and control sites. Plankton samples collected from both sites revealed calanoid copepods, hyperiid amphipods, crab zoea, crab megalopae, and sergestid shrimp were the major constituents.

DISCUSSION

Whale shark aggregations have been reported in association with spawning of a variety of fishes (Gunn et al. 1992, Heyman et al. 2001), corals (Taylor 1994), crabs (Colman 1997), and copepods (Clark and Nelson 1997). The whale sharks observed in this study exhibited behaviors similar to those in Colman (1997) and Heyman et al. (2001) described as surface ram filter feeding, and by

Colman (1997) as 'coughing' to clear or flush gill rakers of accumulated food particles. These observations, when combined with the abundance of fish eggs at the study site and reported feeding of whale sharks on fish eggs by Heyman et al. (2001), indicate that whale sharks in our study area were feeding on the fish eggs. This represents the first confirmed observation of a feeding aggregation of whale sharks in the GOM.

Genetic analysis revealed that egg morph 1 (98% of eggs collected) was little tunny; a finding supported by gonad histology of little tunny caught at the study site. Eggs from little tunny and crevalle jack (2% of eggs collected) were in the mid-embryonic stage of development, indicating recent spawning had occurred at the study site which was located over the only significant shelf edge promontory in the area (Figure 1). Crevalle jack were not observed at the study site during the investigation but are common residents within the area during summer months (S. Schindler, pers. comm., Shore Thing Charters, Bay St. Louis, MS). The constant presence of feeding whale sharks, little tunny eggs, and little tunny in spawning condition over the topographic feature throughout our investigation strongly suggests this was the location of spawning activity which produced eggs collected at the study site.

Previous research has shown that whale sharks occur in areas of enhanced productivity (Iwasaki 1970, Arnborn and Papastavrou 1998, Duffy 2002) and may time their migrations to coincide with localized productivity events to increase feeding opportunities (Wilson et al. 2001). Interestingly, 2 other whale shark aggregations were reported in the vicinity of our study site about 2 weeks prior to (10 June, 15 sharks, D. Bouza, per. comm., Metairie, LA) and following (13 July, >50 sharks, M. Boatner, pers. comm., Tomball, TX) our investigation. The study site was in close proximity to the Mississippi River, which is the greatest source of nutrient input in the GOM (Lohrenz et al. 1990). The mixing of Mississippi River waters with oligotrophic northern GOM oceanic waters, combined with continental slope upwelling (Lohrenz et al. 1990), enhances primary productivity and creates a favorable environment for zooplankton (Grimes and Finucane 1991); a documented food of whale sharks (Clark and Nelson 1997, Colman 1997). The Mississippi River's highest discharge typically occurs during spring and summer (Dinnell and Wiseman 1986); a time that coincides with highest seasonal abundance of whale sharks in the GOM (Burks et al. 2006, Hoffmayer and Franks unpub. data). The north central GOM may provide the most consistent seasonal feeding location for whale sharks in the GOM and may represent a predictable area for their occurrence.

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Jan R. McDowell

Virginia Institute of Marine Science

Jeanette E.L. Carlsson

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John E. Graves

Virginia Institute of Marine Science

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GENETIC ANALYSIS OF BLUE MARLIN (*MAKAIRA NIGRICANS*) STOCK STRUCTURE IN THE ATLANTIC OCEAN

Jan R. McDowell¹, Jeanette E.L. Carlsson², and John E. Graves²

¹Corresponding author. Jan McDowell, Virginia Institute of Marine Science, PO Box 1346, Route 1208 Grete Road, Gloucester Point, Virginia 23062, Phone (804) 684-7263, Fax (804) 684-7263, E-mail mcdowell@vims.edu

²School of Marine Science, Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, Virginia 23062 USA

ABSTRACT The genetic basis of stock structure of blue marlin (*Makaira nigricans* Lacepède 1802) in the Atlantic ocean was inferred from analyses of mitochondrial control region sequences. Blue marlin were collected in 1998 from 4 major geographic locations: western North Atlantic, Caribbean Sea, western South Atlantic and eastern Atlantic. Haplotype diversity (h) ranged from 0.99–1.0 and nucleotide sequence diversity (π) ranged from 0.11–0.13 within samples indicating that the control region harbors a significant amount of genetic variation. However, no significant differences were found in the spatial partitioning of genetic variation among the 4 collections; all pairwise ϕ_{ST} values were negative and were therefore all taken as estimates around a true value of 0. As with previous studies of blue marlin, sequences were comprised of 2 distinct mitochondrial lineages separated by an average of 138 base pairs and ϕ_{ST} between clades of 0.799 ($P < 0.0001$). These 2 lineages were present in similar frequencies across sampling locations. Genetic data from this study support management of Atlantic blue marlin as a single, Atlantic-wide stock.

RESUMEN La base genética de la estructura de poblaciones del marlin azul (*Makaira nigricans* Lacepède 1802) en el Océano Atlántico fue inferido de analiza de sucesiones de región de control de mitochondrial (ADNm). El marlin azul fue reunido en 1998 de cuatro ubicaciones geográficas mayores: el norte occidental del Mar Atlántico, el Mar Caribe, el Atlántico Sur occidental y el Atlántico oriental. La diversidad de haplotipos (h) recorrió de 0,99–1,0, y la diversidad de la sucesión de nucleótido (π) recorrió de 0,11–0,13 dentro de las muestras, que indican que la región del control abriga una cantidad significativa de la variación genética. Sin embargo, ningunas diferencias significativas fueron encontradas en el dividir espacial de la variación genética entre las cuatro colecciones; todos valores de ϕ_{ST} fueron negativos y fueron por lo tanto todo tomado como estimaciones alrededor de un valor verdadero de 0. Al igual que con estudios previos del marlin azul, las sucesiones fueron comprendidas de dos linajes claros de mitochondrial separados por un promedio de 138 pares despreciables y ϕ_{ST} entre clades de 0,799 ($P < 0,0001$). Estos dos linajes fueron presentes en frecuencias semejantes a través de probar las ubicaciones. Los datos genéticos de esta investigación apoyo la administración del marlin azul Alántico como una sola población en Atlántico entero.

INTRODUCTION

The blue marlin, *Makaira nigricans* (Lacepède 1802), is a circumtropically distributed, highly migratory member of the family Istiophoridae that inhabits pelagic waters with surface temperatures above 22° C (Nakamura 1985). In the Atlantic Ocean, blue marlin are considered to be highly over-exploited; the stock was estimated to be at 40% of that needed for maximum sustainable yield at the last complete assessment (ICCAT 2000). Recent indices suggest a continuing decline of the stock abundance through 2004 while other indices suggest a leveling off of the decline (ICCAT 2006). Although more than half of the catch of blue marlin has historically come from the long-line fishery, new artisanal fleets have recently harvested large catches of blue marlin, including a FAD fishery in the eastern Caribbean islands and a fleet of small longliners operating off Brazil between 20°S and 26°S (ICCAT 2006). These new fisheries have heightened concern about the status of the stock and highlighted the need for a bet-

ter understanding of the stock structure of this species throughout the Atlantic Ocean for effective management.

Tagging studies have shown that blue marlin are capable of long distance migrations including trans-oceanic and trans-equatorial movements in both the Atlantic and Pacific oceans as well as inter-oceanic movements (Atlantic to Indian and Pacific to Indian oceans) (Ortiz et al. 2003). Although about 85% of recovered blue marlin were at large for 3 yr or less, analysis of the movement of blue marlin with longer times at liberty (up to 11 yr) found no indication of site fidelity or cyclical annual movements. However, there was evidence of strong seasonal movement patterns in the Atlantic, primarily from the US mid-Atlantic and Mexican Caribbean to Venezuela.

Until recently, spawning areas of blue marlin were not well known. This lack of information stemmed from the difficulty in both collecting and identifying larval istiophorid billfishes to species based on pigmentation and morphometric characters (Richards 1974, Collette et al. 1984, Nishikawa and Rimmer 1987, Nishikawa 1991).

However, recent advances in species-level identification of larval istiophorids have allowed researchers to investigate the temporal and spatial patterns of billfish spawning. Spawning has recently been documented in several locations in the western North Atlantic during the summer months based on the presence of small blue marlin larvae. These areas include Exuma Sound, Bahamas, (Serafy et al. 2003), Straits of Florida (Luthy et al. 2005), Punta Cana, Dominican Republic (Prince et al. 2005), Bermuda (Luckhurst et al. 2006), and the Gulf of Mexico (Jay Rooker, Texas A&M University, pers. comm.).

Evidence of seasonal movement patterns from tagging data combined with new information on the habitat preference and spawning locations of blue marlin in the Atlantic have lead some researchers to hypothesize that blue marlin may exhibit fidelity to spawning grounds. A recent pop up satellite archival tag (PSAT) study off Punta Cana, Dominican Republic (Prince et al. 2005) suggested that reproductively active blue marlin may have a more constrained mean displacement per day in the spawning season than the range exhibited by blue marlin tagged in other localities and seasons (i.e., Graves et al. 2002, Kerstetter et al. 2003). It is not known whether blue marlin revisit the same spawning area in different years. However, taken with evidence from conventional tagging data that other members of the Istiophoridae, such as the striped marlin (Ortiz et al. 2003) and black marlin (Pepperell 1990) exhibit cyclical movements, it is conceivable that blue marlin could exhibit spawning site fidelity. If blue marlin exhibit site fidelity, one would expect this to result in population genetic structure. This issue needs to be examined further.

Previous genetic studies of blue marlin population structure have indicated that the species comprises a single Atlantic-wide population. However, these studies were primarily focused on differentiating Atlantic and Pacific populations of blue marlin, so sampling within the Atlantic was limited (Buonaccorsi et al. 1999, 2001, Graves and McDowell 2001). These studies used whole-molecule mitochondrial DNA (mtDNA) restriction fragment length polymorphism analysis (RFLP), which is less discriminatory than sequencing of individual loci; no comprehensive study based on mitochondrial DNA sequences has been conducted to date. The mitochondrial genome is an ideal candidate for population-level analyses because of its uniparental mode of inheritance and rapid rate of evolution (reviewed in Avise 2001, Hallerman 2003). The mitochondrial genome experiences a rate of nucleotide substitution that has been estimated to approach 5–10 times that of nuclear DNA (Brown et al. 1979, Saccone et al. 1999, Avise 2001) and the non-coding control region, evolves

3–5 times faster than the mitochondrial genome as a whole (Avise 2001). In addition, in the absence of gene flow and assuming an equal rate of mutation, selection and drift, genetic divergence accumulates more rapidly in the mitochondrial genome because it is haploid and uniparentally inherited (Hallerman 2003).

Although multiple classes of molecular markers have been used to look for evidence of population structure in blue marlin, mtDNA was found to be more sensitive to population structuring in this species than either allozymes, single-copy nuclear DNA or microsatellites (Buonaccorsi et al. 2001). Analyses of mtDNA sequence variation have been successfully used to address phylogeographic questions in a number of fish taxa. These include studies pertinent to stock management of pelagic marine fishes such as swordfish, *Xiphias gladius* (Reeb et al. 2000, Alvarado-Bremer et al. 2005), blue marlin, *M. nigricans* (Buonaccorsi et al. 1999), black marlin, *Istiompax indica* (Falterman 1999), sailfish, *Istiophorus platypterus* (Graves and McDowell 1995, McDowell and Graves 2002), white marlin, *Kajikia albida* (Graves and McDowell 2001, 2003, 2006), striped marlin, *K. audax* (Graves and McDowell 1994, 2003), bigeye tuna, *Thunnus obesus* (Chow et al. 2000, Durand et al. 2005, Martinez et al. 2006), bluefin tuna, *T. thynnus* (Carlsson et al. 2004, Alvarado-Bremer et al. 2005), albacore tuna, *T. alalunga* (Vinas et al. 2004), and wahoo, *Acanthocybium solandri* (Garber et al. 2005). In the present study, we analyze mitochondrial control region samples of blue marlin taken throughout their Atlantic range to test the null hypothesis that blue marlin do not exhibit genetic stock structure.

MATERIALS AND METHODS

In this study, 57 blue marlin samples were collected from four major geographic regions: the western North Atlantic (WNA; US mid-Atlantic; $n=15$), the Caribbean Sea (CAR; Jamaica; $n=11$), the western South Atlantic (WSA; southern Brazil; $n=13$) and the eastern Atlantic (EA; Ghana; $n=18$). All samples were collected in the same calendar year (1997–1998) with the exception of 9 of the WNA samples, which were collected in 1995. Samples consisted of either heart tissue removed after capture, cooled on ice, and stored at -80°C , or white muscle preserved in 0.25 mM EDTA pH 8.0, 20% DMSO, and saturated NaCl (Seutin 1991) at room temperature.

Total genomic DNA was extracted from 0.05–0.5g skeletal and/or heart muscle following the methods of Sambrook et al. (2001). Briefly, tissue was digested at 37°C over night with 15 μl proteinase K (25 mg/ml), 15 μl RNase (10mg/ml), 60 μl 10% sodium dodecyl sulfate

(SDS) and 500 µl isolation buffer (50 mM EDTA, 50mM Tris, 150 mM NaCl, pH 8.0). DNA was isolated using a standard phenol extraction procedure and precipitated using an equal volume of isopropanol and 0.04x volume 5 M NaCl. Double-stranded nucleotide sequences from the hypervariable mitochondrial control region were amplified using *Taq* PCR Core reagents (Qiagen Corp. Valencia, CA) with published universal PCR primers DloopK (5' AGCT-CAGCGCCAGAGCGC CCGTC TTGTAAG 3'; Lee et al. 1995), DloopL (5' AGTAAGAGCCCACCATCAGT 3'; Lee et al. 1995), 1CD-Loop(H1) (5' TTGGGTTTCTCG-TATGACCG 3'; Cronin et al. 1993). Each 25 µl PCR reaction contained the following: approximately 5–25 ng purified DNA, 2.5 µl 10X PCR reaction buffer (Tris-Cl, KCl, (NH₄)₂SO₄, 15 mM MgCl₂; pH 8.7), 0.5 µl 10 mM dNTP mix (dATP, dCTP, dGTP, dTTP, 10 mM each), 0.125 µl *Taq* DNA polymerase (5 units/µl), 0.5 µl of 10 mg/ml bovine serum albumin (BSA), and 10 pmoles of each primer. PCR amplification conditions consisted of an initial denaturation of 4 min at 94° C, followed by 35 cycles of 1 min at 94° C, 1 min at 48° C, and 1 min at 72° C, followed by a final extension of 3 min at 72° C. Following electrophoresis, products were visualized using a UV transilluminator. Amplified products were purified by column filtration (QIAquick PCR Purification, Qiagen Corp., Valencia, CA), or by using EXOSAP (USB Scientific, Cleveland, OH) prior to DNA sequencing.

Purified PCR products were sequenced in forward and reverse directions using BigDye Terminator v3.1 Cycle Sequencing reagents (Applied Biosystems, Warrington, UK). Sequencing reactions were composed of 10–50 ng template DNA, 0.25 µl sequencing primer, 0.25 µl BigDye master mix, 1 µl 5x reaction mix and water to a final volume of 5 µl. Cycle sequencing conditions consisted of an initial denaturation of 1 min at 96° C, followed by 25 cycles of 10s at 96° C, 5s at 50° C, and 4 min at 60° C. Primers used for cycle sequencing were identical to primers used in original PCR amplification reactions. Amplification products were electrophoresed on an ABI 3130 sequencer equipped with an 80 cm capillary. Results were analyzed using Sequencing Analysis v. 5.1.1 software (Applied Biosystems, Warrington, UK). Standard chromatogram format (SCF) curves were exported for subsequent analyses and consensus sequences of forward and reverse reactions were created using Sequencer 3.0 (Gene Codes Corp., Ann Arbor, MI). All sequences were subsequently aligned using the Clustal W algorithm (Thompson 1997) in MacVector 7.2 (Accelrys Inc., San Diego CA), with default parameters and adjusted by eye.

Sequence characteristics including base composition and number of substitutions (as well as relative contri-

bution by transitions, transversions, indels) were calculated in Arlequin v 3.1 (Excoffier et al. 2005). A different haplotype designation was given to each unique DNA sequence. Haplotype diversity (h), nucleotide diversity (π) (Nei 1987), and pairwise nucleotide sequence divergence were calculated using Arlequin 3.1 (Excoffier et al. 2005). PAUP* 4.0b10 (Swofford 1999) was used to generate an unweighted pair group method with arithmetic mean (UPGMA, Sneath and Sokal 1973) tree to visualize phylogeographic patterns within this species. In addition, hierarchical analyses of molecular variance (AMOVA) were performed in Arlequin 3.1 to evaluate geographic structuring of molecular variance. Population pairwise ϕ_{ST} values were calculated and used as a proxy of gene flow. All analyses were performed using the Tamura-Nei model (Tamura 1993). For AMOVA and ϕ_{ST} calculations, the probability of significance was assessed using 10000 permutations of the data.

RESULTS

Mitochondrial control region sequences were collected from all 57 blue marlin samples and were deposited in Genbank under accession numbers EF607795-607852. Sequence length ranged from 878 to 891 base pairs (bp) and comprised most of the control region. The final alignment of 904 bp, including indels, exhibited 301 polymorphic sites, 237 of which were parsimony informative. There were 282 transitions, 22 transversions and 39 indels and the transition:transversion ratio was estimated to be 12.8. The relative contribution of each nucleotide was about 32.2% A, 22.8% C, 16.2% G, and 28.9% T; the mean nucleotide composition was biased towards adenine and thymine. Fifty-four of the 57 samples examined had unique haplotypes ($h = 0.9981$, $\pi = 0.1034 \pm 0.050$). Three haplotypes were represented by 2 individuals. These were shared between EA and WNA, between WNA and WSA and within EA. No haplotype was found more than twice. The absolute number of differences between haplotypes ranged from 2 to 166 (mean = 93.45 ± 40.8).

Diversity was high in all collections and the mean number of pairwise differences between individuals randomly drawn from a collection ranged from 99.8 (WNA) to 110.2 (WSA) and nucleotide diversity ranged from 0.115 (WNA) to 0.129 (CAR) (Table 1). These values were similar to those between randomly selected individuals from different collections. The corrected mean pairwise differences between collections were all negative (essentially zero). The global ϕ_{ST} based on Tamura-Nei (1993) distances of -4.61 (essentially zero) was not significantly different from 0 ($P = 0.95624$). Pairwise ϕ_{ST} values were

TABLE 1

Measures of diversity for Atlantic samples of blue marlin, and for groups of alleles comprising the Atlantic (ATL) and ubiquitous (UCL) clades. N refers to the total number of samples. No. Haps refers to the number of distinct haplotypes. h refers to haplotypic diversity, π refers to the nucleotide sequence diversity i.e., the mean number of base pair differences between 2 randomly chosen haplotypes within the sample. $s_{\bar{x}}$ refers to standard error associated with the sampling process.

Location	N	No. Haps	h	$\pm s_{\bar{x}}$	π	$\pm s_{\bar{x}}$
EA	18	17	0.993	± 0.021	0.121	± 0.061
WNA	15	15	1.000	± 0.024	0.115	± 0.059
CAR	11	11	1.000	± 0.039	0.129	± 0.068
WSA	13	13	1.000	± 0.030	0.124	± 0.064
CLADES						
ATL	27	25	0.994	± 0.012	0.0619	± 0.031
UCL	30	29	1.000	± 0.009	0.0170	± 0.009

also all negative and were therefore all taken as estimates around a true value of 0. A UPGMA clustering of the 57 mtDNA control region sequences (Figure 1) did not indicate a significant association of haplotypes with geographic area.

Clade Distribution

Evidence of 2 distinct clades was noted in the UPGMA tree generated from pairwise nucleotide sequence divergence values based on a Tamura-Nei model (Figure 1). Sequences were designated as either Atlantic, referring to sequences found only in the Atlantic, or ubiquitous, composed of sequences found in both Atlantic and Pacific individuals. This designation was based on alignment of sequences with control region sequences taken from 2 individuals from the Pacific, which were known to belong to the ubiquitous clade based on previous RFLP data and by comparison of the RFLP profiles of Atlantic samples known to belong to the Atlantic and ubiquitous clades based on previous studies to their control region sequences. The clades were present in similar frequencies, 47.4% (25 haplotypes) of individuals belonged to the Atlantic clade while 52.6% (29 haplotypes) belonged to the ubiquitous clade. The relative frequencies of Atlantic and ubiquitous clade haplotypes at each sampling location were as follows: WNA 40% Atlantic, 60% ubiquitous, CAR; 45.5% Atlantic, 54.5% ubiquitous; WSA 53.8% Atlantic, 46.2% Ubiquitous and EA; 50% Atlantic and 50% Ubiquitous.

Although the distribution of the clades was relatively homogenous, they had very different diversity indices. The ubiquitous clade was generally much less diverse, having 141 polymorphic sites including 124 transitions and a single transversion, while the Atlantic clade sequences had 210

polymorphic sites with 190 transitions and 9 transversions. Nucleotide sequence diversity within the ubiquitous clade was 1.7% with a mean of $15.18 \pm 6.98 s_{\bar{x}}$ pairwise differences between sequences while nucleotide sequence within the Atlantic clade was 6.2% with a mean of $54.97 \pm 24.5 s_{\bar{x}}$ pairwise differences between sequences. The Atlantic and ubiquitous clades were very divergent from one another. The mean corrected nucleotide sequence divergence between clades was 173.66 (corrected value = 138.01) and the ϕ_{ST} between clades was 0.799 ($P < 0.0001$).

DISCUSSION

Analysis of mtDNA control region sequences of blue marlin taken from throughout their Atlantic range showed no evidence of structuring among locations. This corroborates the results of previous studies of blue marlin demonstrating a lack of detectable structure within the Atlantic. Buonaccorsi et al. (1999) compared three classes of molecular markers with a wide range of mutation rates to look for evidence of population structure within blue marlin taken from three Atlantic and four Pacific locations over five years; although not all collection locations were used for all marker classes. The 2 slower evolving marker classes, scnDNA loci, which were surveyed at 2 Atlantic and four Pacific locations, and allozymes, which were surveyed from 2 Atlantic and a single Pacific location, revealed significant differences in the distribution of allele frequencies between collections from different oceans. Data based on allozymes were insufficient to allow analysis of intra-ocean divergence, but analysis of the scnDNA loci did not reveal significant intra-ocean diver-

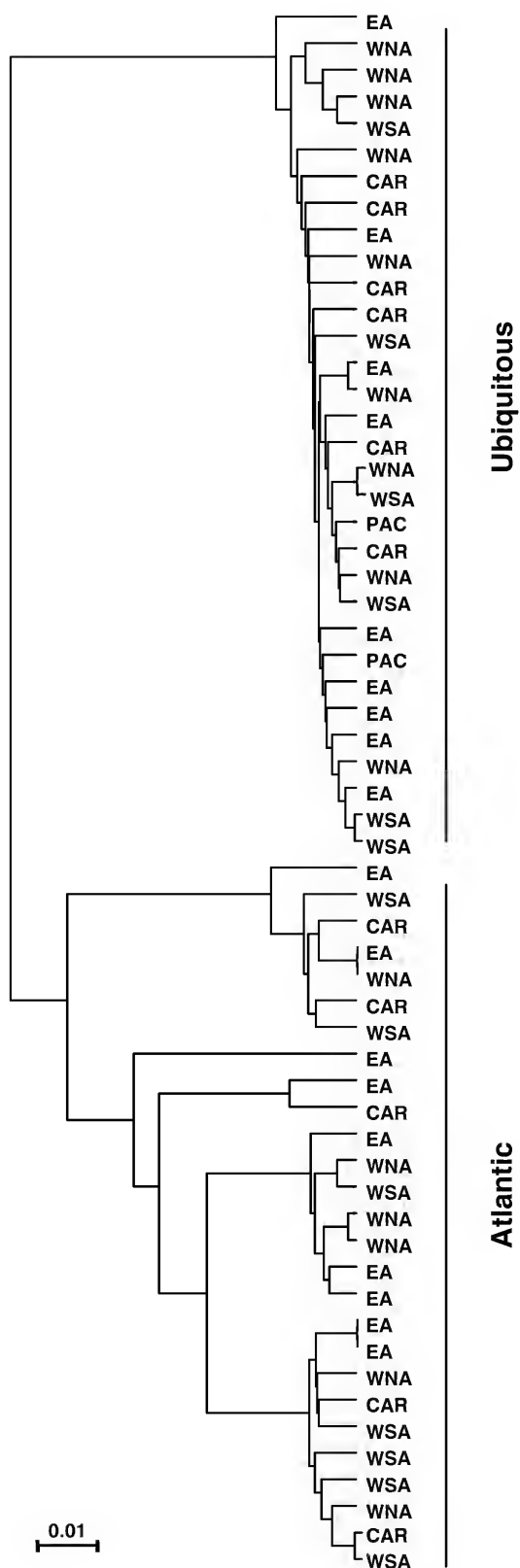


Figure 1. UPGMA tree of blue marlin haplotypes based on a Tamura-Nei distance. Abbreviations are the western North Atlantic (WNA), the Caribbean Sea (CAR), the western South Atlantic (WSA), the eastern Atlantic (EA), and Pacific (PAC).

gence within either ocean. Likewise, RFLP data based on the more rapidly evolving mitochondrial DNA molecule revealed significant inter-ocean divergence. A subsequent study by Buonaccorsi et al. (2001) compared results of previous data with data from five highly polymorphic tetranucleotide nuclear microsatellite markers. Results showed a level of inter-ocean divergence similar to that seen using mtDNA RFLP data, but no effort was made to look at intra-ocean collections; Atlantic collections in the study were limited to samples taken in the Caribbean (Puerto Rico and Jamaica). A later study by Graves and McDowell (2001) used the same loci as Buonaccorsi et al. (1999) and Buonaccorsi et al. (2001) and also included RFLP analysis of the mitochondrial cytochrome *b* and the nuclear RP2 intron gene regions. In addition, the study included samples taken from the eastern Atlantic (Ghana) and western South Atlantic (Brazil). As in previous studies, there was no evidence of significant spatial heterogeneity among Atlantic blue marlin collections. The results of these studies agree that there is a significant barrier to gene flow between Atlantic and Pacific blue marlin populations, but none show evidence of genetic structure within ocean basins.

The lack of observed of genetic stock structure in Atlantic blue marlin in the current study is also consistent with results of tagging studies demonstrating that blue marlin are capable of trans-oceanic and trans-equatorial migrations in the Atlantic as well as fisheries data showing that blue marlin are continuously distributed across the 5°N latitude throughout the year. In addition, data from Nakamura (1985) suggests that blue marlin spawn over a wide area and have a protracted spawning period. This high migratory capability highlights the potential for gene flow. These results are consistent with the results of the recent study of the white marlin by Graves and McDowell (2006), which also failed to detect stock structure based on analysis of genetic data.

The current study was able to overcome some of the limitations of previous investigations, such as a lack sufficient geographic coverage to allow for a robust test of the null hypothesis that blue marlin do not exhibit stock structure within the Atlantic Ocean. In addition, unlike previous studies, this study includes a comparison of samples of blue marlin taken in the same calendar year to eliminate sampling error associated with sampling across multiple years, although each sample in the current study likely included animals spanning several year classes. The current study does have several limitations, including the relatively low samples sizes from each location ($n = 11-18$). It is possible that samples sizes were insufficient to detect genetic structure, although neither the distribution

of haplotypes nor the relationship among haplotypes was significantly associated with collection location. Another potentially more serious problem involves the age of the fish examined. It is possible that blue marlin exhibit genetic stock structure but that this structure may not be evident if fish were sampled from a mixed stock (i.e., on feeding grounds or on migratory routes; see Bowen et al. 2005 for an in-depth discussion). To overcome this limitation, future samples either need to be taken when the stocks are separated i.e., during spawning, or need to be comprised of young animals before they are capable of extensive dispersal. No evidence of sex-biased dispersal was found in a previous study of blue marlin (Buonaccorsi et al. 2001), however the possibility that genetically distinct stocks may mix at certain times has not been examined, and many studies have shown that highly migratory marine species have complex life histories that can confound the presence of underlying structure (Carlsson et al. 2004, Hueter et al. 2004).

As in the present study, previous studies of blue marlin using mitochondrial RFLP analysis revealed the presence of 2 distinct mitochondrial clades, one present only in the samples taken from the Atlantic and one present in both Atlantic and Pacific samples. This pattern of cladogenesis has also been observed in other large pelagics including sailfish (Graves and McDowell 1995, McDowell and Graves 2002), swordfish (Alvarado-Bremer et al. 1996, 2005, Rosel and Block 1996) and bigeye tuna (Chow et al. 2000, Durand et al. 2005, Martinez et al. 2006). The most common explanation for this recurring pattern involves vicariant isolation during the Pleistocene followed by secondary contact via unidirectional migration (Chow et al. 2000, Buonaccorsi et al. 2001, Graves and McDowell 2003, Alvarado-Bremer et al. 2005, Durand et al. 2005).

Although the distribution of clades in this study was relatively even overall (47.4% vs 52.6%), it is interesting to note that the Atlantic clade increased in frequency from 40% to 45.5% to 53.8% moving from north to south in the western Atlantic. Sample sizes were not sufficient to assess whether this trend was statistically significant, however if this pattern remains when larger sample sizes are examined, it would suggest that gene flow is limited. Future studies should examine larval and young-of-year fish before they are capable of dispersing for long distances. However, the current study provides a good baseline to elucidate the amount of genetic variation present and will be invaluable for comparison with larval samples in future studies.

As with previous methods, this study could not disprove the null hypothesis that geographic collections of Atlantic blue marlin were sampled from a single genetic

stock. Based on the data in this study, there is no evidence to suggest that there are discrete stocks of blue marlin in the Atlantic or that blue marlin exhibit spawning site fidelity. This result is consistent with ICCAT's current management of blue marlin as a single Atlantic-wide stock. However, it is important to note that although limited gene flow may be sufficient to prevent the accumulation of genetic divergence, this does not necessarily mean that interactions among blue marlin from different geographic areas are sufficient to prevent regional over-fishing from a management perspective. In other words, although there is little danger that over-harvesting of blue marlin from a single area will remove unique genetic variation, it is not possible to predict the rate at which migrants would supplement a locally depleted stock from this genetic analysis.

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Nocturnal Depth Distribution of Western North Atlantic Swordfish (*Xiphias gladius*, Linnaeus, 1758) in Relation to Lunar Illumination

Joshua K. Loefer

South Carolina Department of Natural Resources

George R. Sedberry

South Carolina Department of Natural Resources

John C. McGovern

NOAA Fisheries Service

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NOCTURNAL DEPTH DISTRIBUTION OF WESTERN NORTH ATLANTIC SWORDFISH (*XIPHIAS GLADIUS*, LINNAEUS, 1758) IN RELATION TO LUNAR ILLUMINATION

Joshua K. Loefer^{1*}, George R. Sedberry¹, and John C. McGovern²

¹South Carolina Department of Natural Resources, Marine Resources Research Institute, PO Box 12559, Charleston, South Carolina 29422-2559, USA

*Corresponding author. Phone (843)953-9060, FAX (843)953-9820, E-mail loeferj@dnr.sc.gov

²NOAA Fisheries Service, 263 13th Avenue South, Saint Petersburg, Florida 33701 USA

ABSTRACT Swordfish are known to undergo large diel vertical movements from surface waters at night to >300 m depth during the day. Evidence presented over the past several decades suggests the lunar cycle affects these vertical migrations. This study collected data concurrently from 7 swordfish throughout 3 consecutive lunar cycles using pop-up satellite archival tags. All individuals demonstrated an inverse relationship between recorded nocturnal depths and lunar illumination.

RESUMEN Los peces espadas son reconocidos por experimentar extensas migraciones verticales desde la superficie durante la noche, hasta aguas profundas (>300 m) durante el día. La evidencia presentada durante las pasadas décadas expone que el ciclo lunar afecta estas. Este estudio presenta la información que ha sido recopilada recientemente de 7 peces espadas durante 3 ciclos lunares consecutivos utilizando etiquetas de archivos que resurgen a la superficie y envían toda la información al satélite, conocidos en inglés como “pop-up satellite archival tags.” Todos los individuos demostraron una relación inversa entre los datos obtenidos para profundidades documentadas en las horas nocturnas e.

INTRODUCTION

The swordfish (*Xiphias gladius*, Linnaeus, 1758) has a worldwide distribution in tropical, sub-tropical and temperate oceans, and its palatable flesh makes it a highly valued commodity throughout its range. The commercial importance of this species has lead to a substantial amount of research on life history, movements, stock identification, and bycatch issues (Ward et al. 2000).

Swordfish are known to undergo large diel vertical migrations characterized by descent to depths of up to 600 m or more during daylight hours and ascent to shallower waters at night (Carey and Robison 1981, Carey 1990). Therefore, most swordfish fisheries target the species at night when they are generally closest to the surface. Draganik and Cholyst (1988) and di Natale and Mangano (1995) noted variation in swordfish catch rates during the full moon in central Atlantic and Italian waters, respectively. de la Serna et al. (1992) found CPUE maximums during the new moon in the Strait of Gibraltar and adjacent Mediterranean and Atlantic waters. Moreno et al. (1991), however, found no relation between moonlight intensity and swordfish abundance, and Manday (1964) also concluded there was no lunar effect on depth-related catch in Cuban waters. Though some of these reports document changes in swordfish catch rate or abundance in relation to the lunar cycle, the methodologies used cannot provide demonstrative evidence that these variations are a direct result of behavioral changes in swordfish. Variations in

CPUE or total catch may be due to designed or unintentional variation in depth of the fishing gear, changes in gear configuration related to tidal currents associated with lunar phase, visibility of bait that might be affected by lunar phase, or lunar periodicity in the behavior of the swordfish or its prey. Electronic tagging provides one of the best available methods to document vertical movements in large pelagic predators such as swordfish and investigate long-term (> 30 d) cyclical behavioral changes.

There have been several published studies on electronic tagging of swordfish (Carey and Robison 1981, Carey 1990, Sedberry and Loefer 2001, Takahashi et al. 2003). However, the study by Carey and Robison (1981) was the only one to mention changes in vertical movement patterns associated with the lunar cycle. They noted that of 6 swordfish tracked using acoustic telemetry, the 3 fish tracked during the full moon occupied deeper nocturnal depths than individuals tracked during other lunar phases. Limitations in study duration imposed by acoustic tracking, however, precluded tracking an individual specimen for an entire lunar cycle. Therefore, their observations on lunar differences had to be inferred from differences in behavior between different individuals, tracked at different times, and, in some cases, different locations.

Pop-up satellite archival tags (PSATs) allow for longer-term fishery independent data collection from highly-migratory fish species than was previously feasible. These devices allow researchers to collect large amounts of vertical movement data from individuals over large time

TABLE I

Tag deployment and pop-up information for all swordfish in the study. DAL = days at large (days from tag deployment to first satellite contact), LJFL = lower jaw fork length.

Tag ID#	Study interval (mos)	Deployment location	Deployment date	Pop-up location	Pop-up date	DAL	Est. LJFL (cm)
28662	1	32°6.4'N, 78°34.2'W	4/18/2002	32°19.6'N, 78°45.4'W	04/28/02	10	91
28663	1	32°2.8'N, 78°25.1'W	4/16/2002	34°17.6'N, 74°45.7'W	04/21/02	5	183
28664	1	32°4.0'N, 78°39.2'W	5/17/2002	32°21.2'N, 78°16.5'W	06/17/02	31	152
28665	1	32°3.4'N, 78°43.8'W	5/7/2002	35°2.0'N, 74°52.9'W	06/07/02	31	122
28666	2	32°4.5'N, 78°43.5'W	5/7/2002	34°31.6'N, 75°37.0'W	07/07/02	61	137
28668	2	32°0.0'N, 78°23.8'W	4/17/2002		No contact		112
28669	2	32°7.1'N, 78°33.3'W	4/18/2002	32°50.9'N, 77°28.7'W	04/27/02	9	213
28670	3	32°2.4'N, 78°41.3'W	5/17/2002	31°37.0'N, 78°29.8'W	08/17/02	92	107
28671	3	32°7.6'N, 78°32.1'W	4/17/2002	34°40.1'N, 75°32.9'W	04/25/02	8	102
30035	3	32°7.0'N, 78°40.9'W	5/7/2002	32°14.3'N, 78°5.6'W	05/12/02	5	122
30036	3	32°4.1'N, 78°24.5'W	4/16/2002	28°59.0'N, 79°58.1'W	07/16/02	91	81
30037	4	32°3.7'N, 78°37.2'W	4/17/2002	33°31.9'N, 75°14.6'W	04/23/02	6	107
30038	4	32°1.9'N, 78°42.4'W	5/16/2002	32°1.3'N, 79°0.0'W	09/16/02	123	107
30039	4	31°58.9'N, 78°45.8'W	5/7/2002	37°46.7'N, 70°51.6'W	08/17/02	102	122
30040	4	31°58.9'N, 78°45.8'W	5/7/2002	33°49.9'N, 76°30.2'W	05/16/02	9	122

periods without the need for recapture. This study presents PSAT data collected concurrently on several swordfish through 3 consecutive lunar cycles in the western North Atlantic.

MATERIALS AND METHODS

Swordfish were captured with pelagic longline gear deployed from a research vessel between 16 April and 17 May 2002. A total of 15 swordfish with estimated lower-jaw fork lengths from 81 to 213 cm were fitted with satellite pop-up tags. Tags were attached to the subjects by harpooning a 6.25 cm titanium M-type dart anchor into the dorsal musculature about 5 cm below the midline of the base of the dorsal fin. The anchors were inserted using a 20 cm titanium tagging needle protected by a 6 cm diameter rubber stopper that limited penetration depth to 12 cm. Tags were tethered to the anchors with 30 cm of 1.66 mm diameter fluorocarbon monofilament leader (100 kg tensile strength). Swordfish were not removed from the water during tagging, and were released by cutting the monofilament hook leader within a few cm of the hook.

Satellite pop-up tags (model PTT-100 Archival pop-up tag, manufactured by Microwave Telemetry, Inc., Columbia, MD, USA) were programmed to jettison at intervals of 30 ($n=4$), 60 ($n=3$), 90 ($n=4$) or 120 ($n=4$) days following tagging. The tags archived temperature and

pressure readings once each hour until the release date was reached. A more complete description of the programming and function of the model PTT-100 PSAT can be found in Loefer et al. (2005).

Depth data retrieved from 7 of the 15 tags were combined and the resulting dataset was filtered so that only depth readings recorded between 0500 and 0900 GMT during the period of greatest temporal data overlap between individuals (8 May 2002 to 15 August 2002) remained. The 0500 to 0900 GMT timeslot was selected because depth data were consistently shallowest during this time period. A mean was calculated for each hourly timeslot in the filtered dataset. Each hourly mean was calculated from 2 to 7 concurrent depth readings from individual PSATs. These data were then compared to a corresponding lunar illumination schedule calculated by the United States Naval Observatory (<http://aa.usno.navy.mil>). Mean nightly depths were then regressed on percent lunar illumination and a correlation coefficient was calculated.

RESULTS

The 15 tags deployed in this study collected a total of 533 d of data while attached to the study animals, of which 462 d (87%) were retrieved via satellite. Six of the 15 tags stayed attached throughout the entire study interval and released on schedule. A total of 8 tags released before the

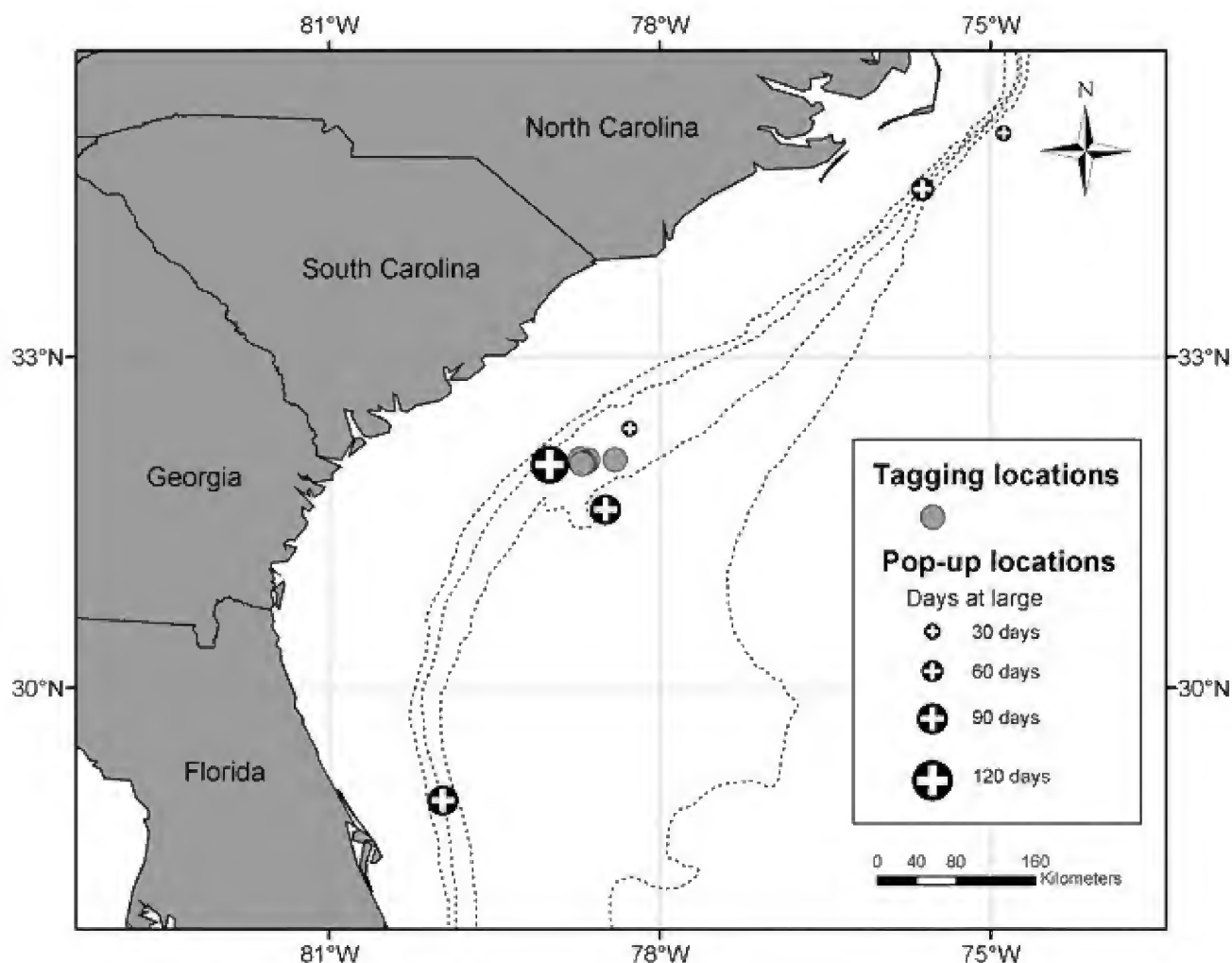


Figure 1. Swordfish tagging and tag pop-up locations ($n=6$). Depth contours (from inshore to offshore) represent 100, 200, 500, and 1000 m.

scheduled date, and one tag never made satellite contact. Examination of data from the 8 early-release tags suggested that 3 were due to immediate post-release mortality, 4 were due to tag shedding (from 4 to 98 d after attachment), and the cause for the early release of one tag could not be determined from the recovered data (Table 1). Pop-up location data for the 6 full-retention tags indicated variation in general directions of movement. One fish moved south (360 km straight-line distance), 2 moved northeast (390 and 490 km), and 3 were within 50 km of the tagging location after up to 120 d at large (Figure 1).

Archived data from the 6 full-retention tags, as well as the tag which shed after 98 d of attachment, showed a strong pattern of diel vertical migrations. Swordfish occupied shallower waters from 0 to 160 m at night, and migrated to depths of 350 to 770 m during the day. They began to ascend from depth around 2–3 h before

sunset (between 0000–0025 GMT in the study area), and they remained in near-surface waters for about 4–6 h. Swordfish usually began to descend before the first post-sunrise hourly record (sunrise: 1008–1040 GMT). The filtered (0500–0900 GMT) data demonstrated an inverse variation between mean nocturnal depths and percent lunar illumination throughout the 3-mo study period (Figure 2). Nocturnal depths recorded during periods of $\geq 90\%$ lunar illumination ranged from 0 to 172 m with a mean of 77.0 m ($n = 443$), while depths recorded when lunar illumination was $\leq 10\%$ were between 0 and 142 m with a mean of 34.3 m ($n = 408$, Figure 3). Linear regression of mean nightly depths on percent lunar illumination demonstrated a significant relationship ($n = 99$, $P < 0.001$) with a correlation coefficient of -0.66 .

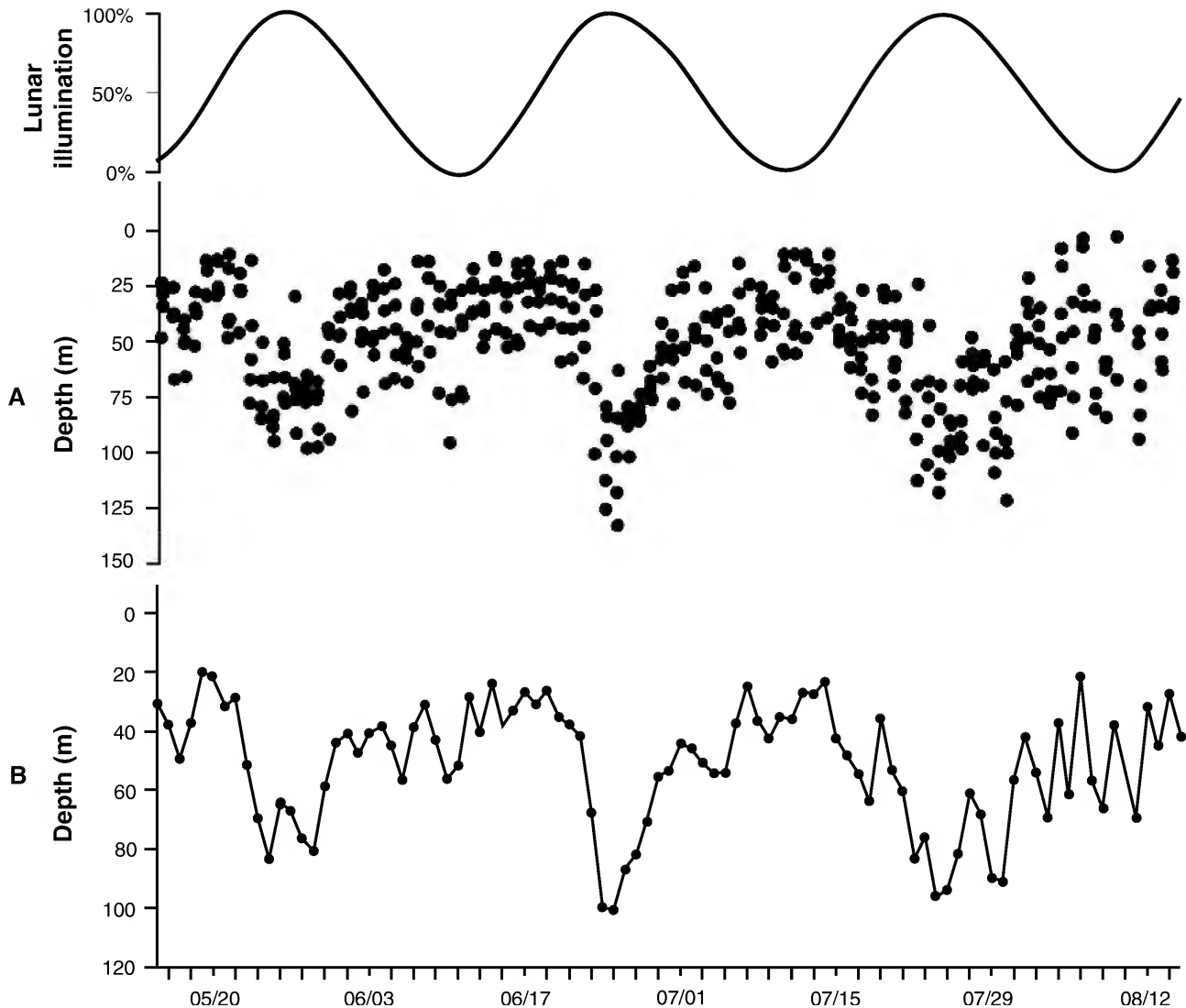


Figure 2. Lunar illumination schedule compared to (A) hourly mean of nocturnal depths ($n = 501$) and (B) nightly depth mean ($n = 99$).

DISCUSSION

Stillwell and Kohler (1985) found that swordfish diet in the western North Atlantic consists primarily of cephalopods (82% by frequency of occurrence) and teleosts (53%), many taxa of which are known to make nocturnal migrations into the shallow mixed layer to feed (Brodziak and Hendrickson 1999, Kinzer and Shulz 1985, Roper and Young 1975, Walker and Nichols 1993). Changes in nocturnal swordfish behavior, therefore, may be a result of active predation on vertically migrant midwater cephalopods and fishes. Swordfish may also follow isolumes to immerse themselves in an environment for which their eyes are adapted for maximum visual acuity and hunting success (Warrant 2004).

Regardless of the reason for these cyclical changes, the theory that swordfish follow isolumes and that their vertical migrations are affected by the lunar cycle is not new. It has long been considered common knowledge among commercial fishermen and fishery workers that swordfish are found further from the surface at night during the full moon than during other lunar phases. However, this conclusion has been based on data collected over a small time frame (less than one full lunar cycle, Carey and Robison 1981), on comparisons between different individuals observed at different times (Carey and Robison 1981), on analysis of CPUE data (Draganik and Cholyst 1988, Moreno et al. 1991, di Natale and Mangano 1995), or on anecdotal observations from fishermen (Manday 1964, di Natale and Mangano 1995). In contrast, the data for this study were collected concurrently from multiple individual fish throughout 3 consecutive lunar

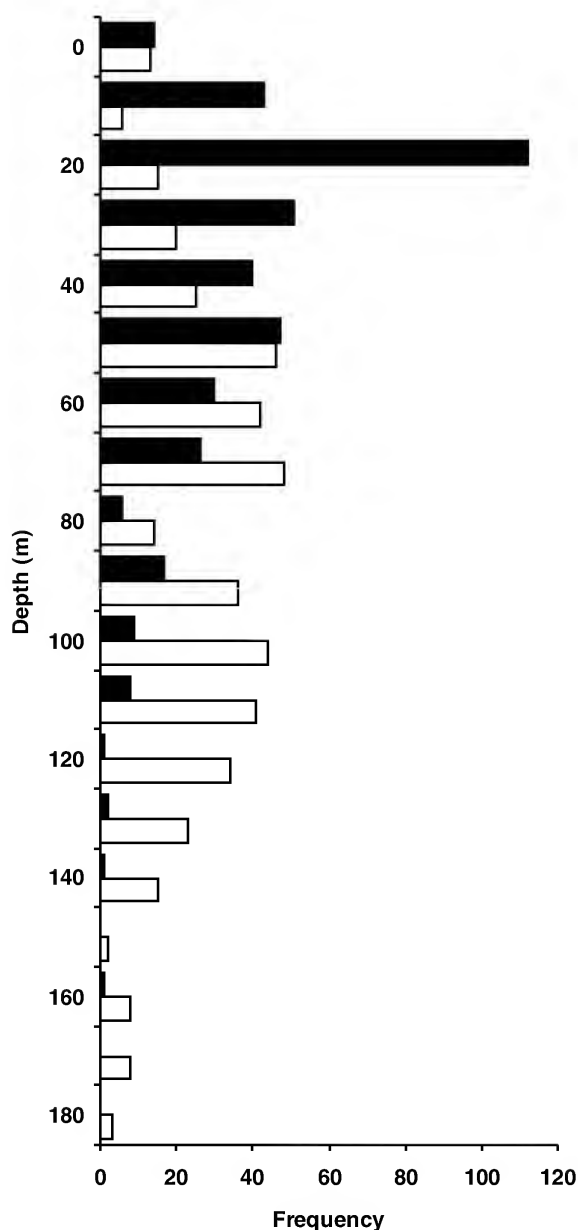


Figure 3. Depth frequency distribution for nocturnal depths ($n = 851$) recorded between 0500 and 0900 GMT during new moon ($\leq 10\%$ lunar illumination, black bars) and full moon ($\geq 90\%$ lunar illumination, white bars).

cycles. The described behavior was ubiquitous despite the movement of several animals away from the tagging area during the study. It is also interesting to note that the correlation between nightly depth and lunar illumination remained intact even when the moon was not visible in the study area (had not risen or had previously set) during the 0500 to 0900 GMT window examined. The data presented thus provide confirmation of the long accepted, yet unproven, theory that changes in nocturnal swordfish depth distributions are correlated with the lunar cycle.

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Richard T. Kraus

George Mason University

Jay R. Rooker

Texas A&M University, Galveston

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PATTERNS OF VERTICAL HABITAT USE BY ATLANTIC BLUE MARLIN (*MAKAIRA NIGRICANS*) IN THE GULF OF MEXICO

Richard T. Kraus¹ and Jay R. Rooker²

¹George Mason University, 4400 University Drive, MSN 5F2, Fairfax, VA 22030 USA, E-mail rkraus1@gmu.edu

²Texas A&M University, 5007 Avenue U, Galveston, Texas 77551 USA

ABSTRACT We examined data from pop-up archival transmitting (PAT) tags ($n = 18$) to characterize aspects of vertical habitat use by blue marlin (*Makaira nigricans*) from the Gulf of Mexico (GOM). Two of these tags were recovered and provided fine-scale information about diving patterns and the relationship between time at depth and temperature. Similar to previous studies, blue marlin in the GOM spent most of their time at the surface and at temperatures within 3° C of surface temperatures. Time at depth was multimodal and the magnitude of the smaller modes was dependent upon the strength and depth of the thermocline. Importantly, time at depth was a complex function of the temperature change relative to the surface, time of day, lunar phase, and water column structure. Temperature change with depth between the western and eastern GOM and the adjacent western Atlantic Ocean was also examined. The depth range (maximum depths varied between 68 and 388 m) varied widely between fish and did not appear to correspond with any particular magnitude of temperature change relative to the surface. Although these data may help to improve stock assessments that are based upon habitat standardizations of CPUE, progress will be limited until the distribution of feeding activity with depth and other aspects of blue marlin behavior in relation to capture probability are elucidated.

RESUMEN Examinamos los datos de marcas archivo por satélite (PAT) ($n = 18$) para caracterizar los aspectos del uso vertical del hábitat por el atún azul (*Makaira nigricans*) del Golfo de México (GOM). Dos de estas marcas fueron recuperadas y proporcionaron información a la escala fina acerca de los patrones de zambullir y la relación entre tiempo en la profundidad y la temperatura. Semejante a estudios previos, el atún azul en el GOM gastó la mayor parte de su tiempo en la superficie y en zonas dentro de 3°C de temperaturas en la superficie. El tiempo en la profundidad fue multimodal y la magnitud de los modos más pequeños fueron dependientes sobre la fuerza y la profundidad del termoclino. Importante, el tiempo en la profundidad fue una función compleja referente al cambio de la temperatura a la superficie, el tiempo de día, de la fase lunar, y de la estructura de la columna de agua. El cambio de la temperatura con la profundidad entre el GOM occidental y oriental y el Océano Atlántico occidental adyacente fue examinado también. La gama de la profundidad (las profundidades máximas variaron entre 68 y 388m) varió extensamente entre pez y no apareció corresponder con ninguna magnitud particular del pariente del cambio de la temperatura a la superficie. Aunque estos datos puedan ayudar a mejorar las evaluaciones de acciones que son basadas sobre estandarizaciones de hábitat de CPUE, el progreso será limitado hasta que la distribución de actividades alimentarios con la profundidad y otros aspectos de la conducta de la atún azul en la relación a la probabilidad de captura es aclarada.

INTRODUCTION

Atlantic blue marlin (*Makaira nigricans*) have been exploited extensively for recreation and by commercial longline fisheries, and current assessments indicate that the stock is overfished and biomass is well below the level that would support a maximum sustained yield (ICCAT 2006). More importantly, assessments indicate that fishing mortality may be fluctuating around the level that would allow year-to-year replacement of biomass lost to fishing (ICCAT 2006). Since fishery-independent data upon which to base assessments of blue marlin are limited, catch per unit effort (CPUE) indices from commercial longline fisheries are a key input for population models. Thus, important efforts have been directed at understanding the relationship between habitat use and the probability of capture on longline gear (Suzuki et al. 1977, Suzuki 1989, Hinton and Nakano 1996, Goodyear 1999, Luo et al. 2006).

One widely applied concept is that CPUE indices can be standardized using environmental data and information about behavior of species such as blue marlin. Goodyear et al. (2003) pointed out that this habitat standardization approach to refining CPUE indices is fraught with problems, most of which reflect an inadequate knowledge of the biology and ecology of fishes caught on longlines. One of the many research needs identified by Goodyear et al. (2003) was a better understanding of vertical habitat use based upon temperature and depth (two of the most commonly measured habitat variables). Brill and Lutcavage (2001) postulated that differences in temperatures experienced by billfish from different locations would not reflect varying temperature preferences but rather selection of the warmest temperatures available, which usually occur at the surface. Saito et al. (2004) presented support for this hypothesis with electronic tag data from the tropical Atlantic. In addition, Graves et al. (2002, 2003) reported

that the distribution of time at temperature and depth was multi-modal for blue marlin with high proportions of time spent in the warmer surface mixed layer. Smaller but pronounced peaks of time spent at depth were observed and were assumed to represent important feeding zones. The multi-modal distribution of time at depth (and temperature) was also substantiated by earlier telemetry studies from the tropical Pacific (Holland et al. 1990, Block et al. 1992). Finally, other restrictions to vertical habitat use, such as dissolved oxygen concentration in the oxygen minimum layer, may limit the depth distribution of blue marlin, albeit dissolved oxygen is probably not a limitation in the western Atlantic Ocean (see Prince and Goodyear 2006).

Here, we contribute to efforts to characterize the vertical habitat use of Atlantic blue marlin, presenting data from 18 pop-up archival transmitting (PAT) tags deployed in the GOM between 2003 and 2005. Regional differences in time at depth and time at temperature were examined using all tags. Two of these tags were recovered, providing fine-scale information (1 min intervals) on temperature and depth histories of blue marlin from regions within and outside the Loop Current. Archival data from recovered tags were also used to examine effects of day and lunar period on vertical patterns of habitat use.

MATERIALS AND METHODS

Blue marlin (size range: 45–81 kg, mean = 93.4 kg) were caught on sport fishing gear, and PAT tags were deployed in a manner similar to Squire (1987) and Chaprales et al. (1998), using either a titanium chevron anchor provided by the tag manufacturer or the nylon anchor described in Domeier et al. (2005). Tags were PAT3 and PAT4 models (Wildlife Computers, Inc., Redmond, Washington). Tags were deployed opportunistically between May and August in 2003 ($n = 3$), 2004 ($n = 9$), and 2005 ($n = 9$) in the northern GOM (within the U.S. exclusive economic zone), and programmed deployment durations were 30 ($n = 5$), 90 ($n = 4$), and 180 d ($n = 12$). Seven of the tags detached prematurely and transmitted data (durations ranged from 12 to 109 d), and 3 additional tags never transmitted (programmed durations were 180 d). Out of 1482 deployment days (excluding tags that did not transmit), 713 d (representing 18 tags) of summarized data were transmitted via satellite, had contemporaneous temperature, depth and light level measurements, and were used for this analysis.

Short-term changes in vertical movements in the recovered tags were examined by plotting depth as a function of time. The temperature time-series from the recovered tags were smoothed and overlaid on the depth

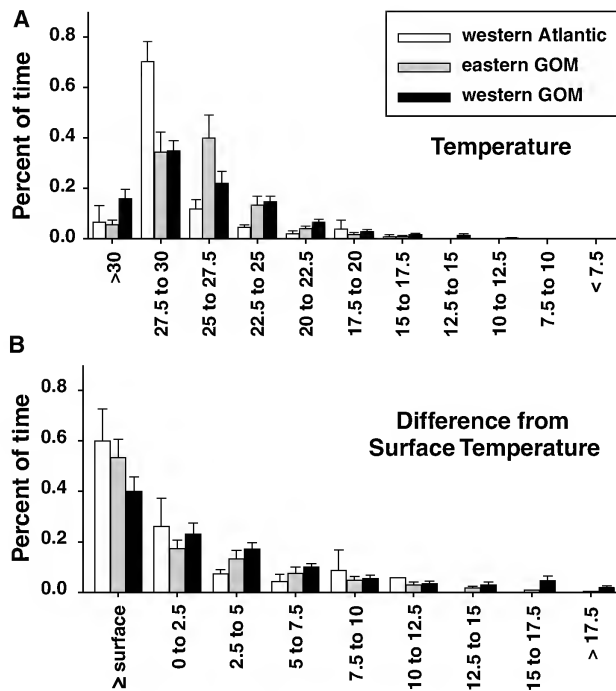


Figure 1. Percent of time as a function of temperature (A) and temperature relative to the surface temperature (B) for Atlantic blue marlin ($n = 18$). Plots were constructed with summarized data transmitted via satellite from pop-up archival transmitting (PAT) tags, and standard error bars show variability between individual fish. Sub-regions are described in the text.

data to view water column structure, and diel patterns were assessed by determining day and night from the light level measurements. Lunar phase was determined from published almanacs based upon date. Longer-term (seasonal) patterns were explored with the satellite-transmitted data; however, patterns (if present) were too variable to discern, and thus not addressed here.

To understand how both depth and temperature delineate blue marlin habitat, recovered tag data were used to calculate the percent of time as a function of both depth and change in temperature relative to the surface temperature. Temperature change was calculated as the difference between the temperature at depth and the most recently adjacent surface (< 2 m) temperature in the series (this approach accommodated for changes in surface temperature throughout the day on each dive). For the satellite-transmitted data, time-at-temperature summaries were based upon 2.5 degree bins, and the percent of time was calculated as a function of both temperature and change in temperature at depth. In addition, we also plotted the change in temperature (relative to the surface, < 2 m) with depth based upon daily surface temperature means.

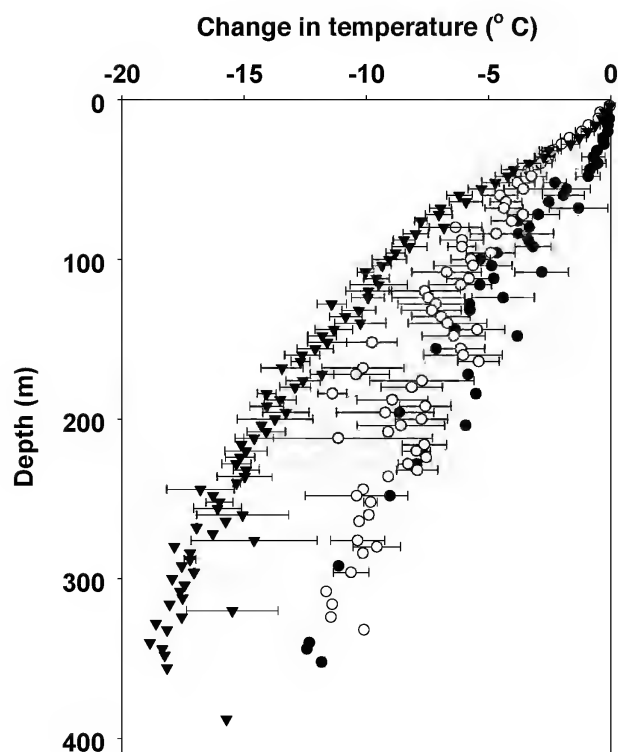


Figure 2. Change in temperature with depth for Atlantic blue marlin ($n = 18$) in the western GOM (filled triangles), eastern GOM (open circles) and adjacent western Atlantic (filled circles). Standard error bars show variability between individual fish. Some combinations of change in temperature and depth were only observed for one blue marlin, thus some points have no error bars (mostly at depths > 150 m). Sub-regions are described in the text.

Finally, to understand large-scale spatial patterns, we divided data based upon sub-regions with longitude values that were estimated using standard algorithms (see Hill 1994, Welch and Eveson 1999) and refined using the Kalman filter tools developed by Sibert et al. (2003) and Nielsen et al. (2006). Sub-regions were arbitrarily chosen to divide the GOM roughly in half at 90°W longitude. We also accounted for locations in the western Atlantic (only one fish showed movement into the Atlantic through the Straits of Florida) by defining a third category for longitudes $< 81^{\circ}\text{W}$. Uncertainty in longitude estimates from light-sensor data is typically $< 1^{\circ}$ (Musyl et al. 2001); therefore, it is important to note that locations west of 90°W are definitively within the GOM, those between 90°W and 81°W are not differentiated between the GOM and the Caribbean Sea, and those east of 81°W are generically in the western Atlantic. The estimated latitudes and the inferred horizontal movement patterns are the subject of a separate manuscript (Kraus and Rooker, in preparation).

RESULTS

Summarized data transmitted by satellite reflected the distinct water column structures found within the three sub-regions: western GOM and eastern GOM and the western Atlantic. The data were classified according to the 2.5°C time-at-temperature bins, and in terms of the absolute temperature, the mean varied by sub-region (Figure 1). In the western GOM and in the western Atlantic, the highest percent of time was spent at temperatures between 27.5° and 30°C (Figure 1a). By comparison, blue marlin in the eastern GOM spent more time at cooler temperatures from 25° to 27.5°C (Figure 1a). These sub-regional differences were not evident when the temperatures were expressed relative to the surface temperature, indicating that blue marlin spent most of their time at the highest temperatures available (i.e., at the surface or within 2.5°C of the surface temperature, Figure 1b). The satellite-transmitted data also demonstrated sub-regional differences in the relationship between depth and change in temperature with depth (Figure 2). West of 90°W longitude, temperature declined rapidly with depth as compared to locations east of 81°W longitude. Intermediate values of change in temperature with depth were observed in the eastern GOM between 81° and 90°W longitudes. As this intermediate area also contains the Loop Current (intrusion of the North Atlantic western boundary current; see Sturges 1993), the water column structure is more variable. Thus, the values recorded by PAT tags showed larger standard errors than in the other sub-regions (Figure 2). It is not clear that either change in temperature or depth presented limitations to blue marlin habitat when comparing sub-regions. Maximum depths ranged between 68 and 388 m between individual fish, and associated temperature changes (relative to the surface) increased linearly with depth, ranging from 5.5° to 18.1°C and showing no apparent limitation with temperature. Finally, there were wide variations between individual fish in the functions of percent of time at depth (Figure 3). Overall, blue marlin spent at least 57% of time at depths < 50 m and at least 78% of time at depths < 100 m, but the high variability indicates that depth alone is a poor predictor of how much time blue marlin will spend in a given water column stratum.

More detailed short-term changes in diving behavior observed from recovered tags were remarkably different between individuals tagged in the western versus the eastern GOM (refer to Figures 4 and 5 for this paragraph). For the fish released in 2004 in the western GOM, there were prominent diel differences in diving behavior with repeated dives and extended periods spent between 30 and 60 m during the day (Figure 4). This range of depths coin-

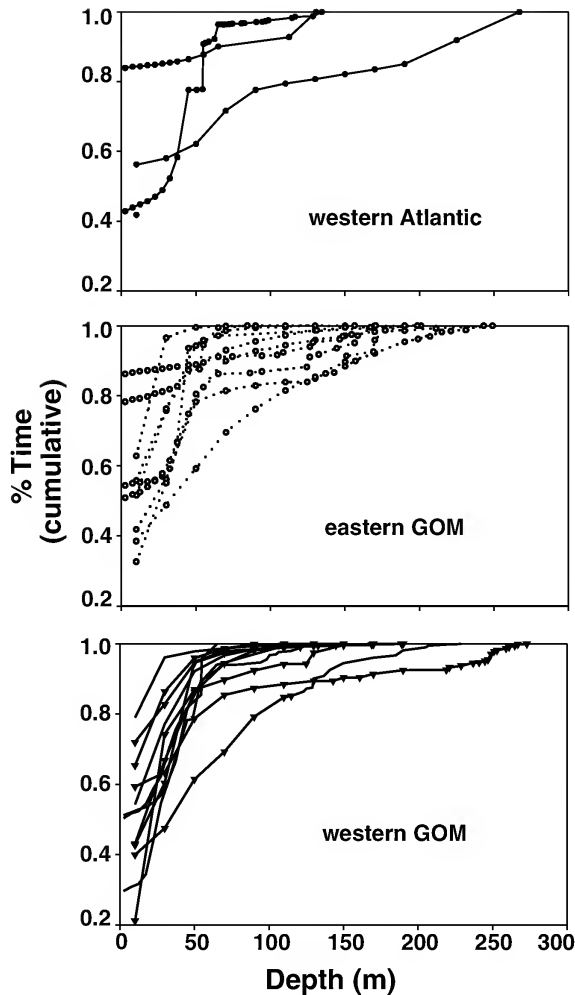


Figure 3. Cumulative percent of time as a function of depth for individual Atlantic blue marlin in different sub-regions (defined in the key) as observed from satellite-transmitted PAT tag data.

cided with a strong thermocline marked by a temperature decline from 28° to 22° C. During the first week at large, the thermocline was more diffuse than in the latter part of the track (the 22° C isotherm occurred between 70 and 80 m during the first 4 d), and the character of the diving pattern was different with slower dives to greater depths early in the track. The first 48 hr of the track should be considered with caution, as this period may represent behavior associated with recovery from tagging and not typical blue marlin diving behavior. Although most of the time in the latter part of the track was spent at or above the thermocline, there were infrequent, short dives below the thermocline. In addition, the diel patterns of diving showed correspondence with lunar phase, in which there was increased diving activity on the night of the full moon and the preceding night. Night-time diving activity was less frequent on the nights prior to and following this period.

By comparison, the fish released in the eastern GOM in 2005 experienced a broad vertical temperature gradient (i.e., the temperature changed from 28° to 22° C between the surface and 300m) and exhibited different diving behavior (Figure 5). The range of depths utilized by this fish was twice that of the fish in the western GOM, and diel changes in diving behavior (if present) were evident only for specific instances (e.g., between the day and night on June 5th). Otherwise, there was little evidence of a diel or lunar pattern, and dives tended to be slower and to greater depths than for the fish in the eastern GOM.

In terms of the percent of time spent as a function of depth and the change in temperature, both of the recovered tags demonstrated that the greatest amount of time was spent at the warmest temperatures available. The top 2 m of the water column and temperatures within 0.5 degrees of the surface represented 62.3% and 88.5% of the total track time for the tags in the eastern and western GOM, respectively. The pattern with depth was also multimodal, especially for the individual tracked in the western GOM. The percent of time spent at depths between 30 and 60 m, and temperatures within 3 degrees of the surface temperature represented 15.9% of the total track time for the tag in the western GOM, whereas this range of values accounted for only 1.8% of the total track time in the eastern GOM. For both of the recovered tags, the remaining proportions of time were spread out over depths up to 150 and 310 m in the eastern and western GOM, respectively in 2004 and 2005 (Figure 6). Temperature differences (relative to the surface) were similar between these fish and no significant amount of time was spent at temperatures > 12 degrees less than the surface temperature (Figure 6).

DISCUSSION

The PAT tags deployed in this study have provided some important insights to the variability in vertical habitat use by blue marlin from a previously overlooked region of the North Atlantic, the GOM. Using temperature and depth as variables that partially describe the habitat of blue marlin, our results further substantiate that the percentage of time spent at depth is closely linked to the temperature change relative to the surface (Brill and Lutcavage 2001, Saito et al. 2004), with the vast majority of time spent at temperatures within 3° C of the surface temperature. There is no reason to expect that size of blue marlin would influence this pattern (the so-called thermal-inertia hypothesis). Because the heart receives blood directly from the gills (where blood rapidly cools to ambient temperature), its temperature (and hence swimming performance) will be nearly identical to the water and will vary independently of

BLUE MARLIN VERTICAL HABITAT USE

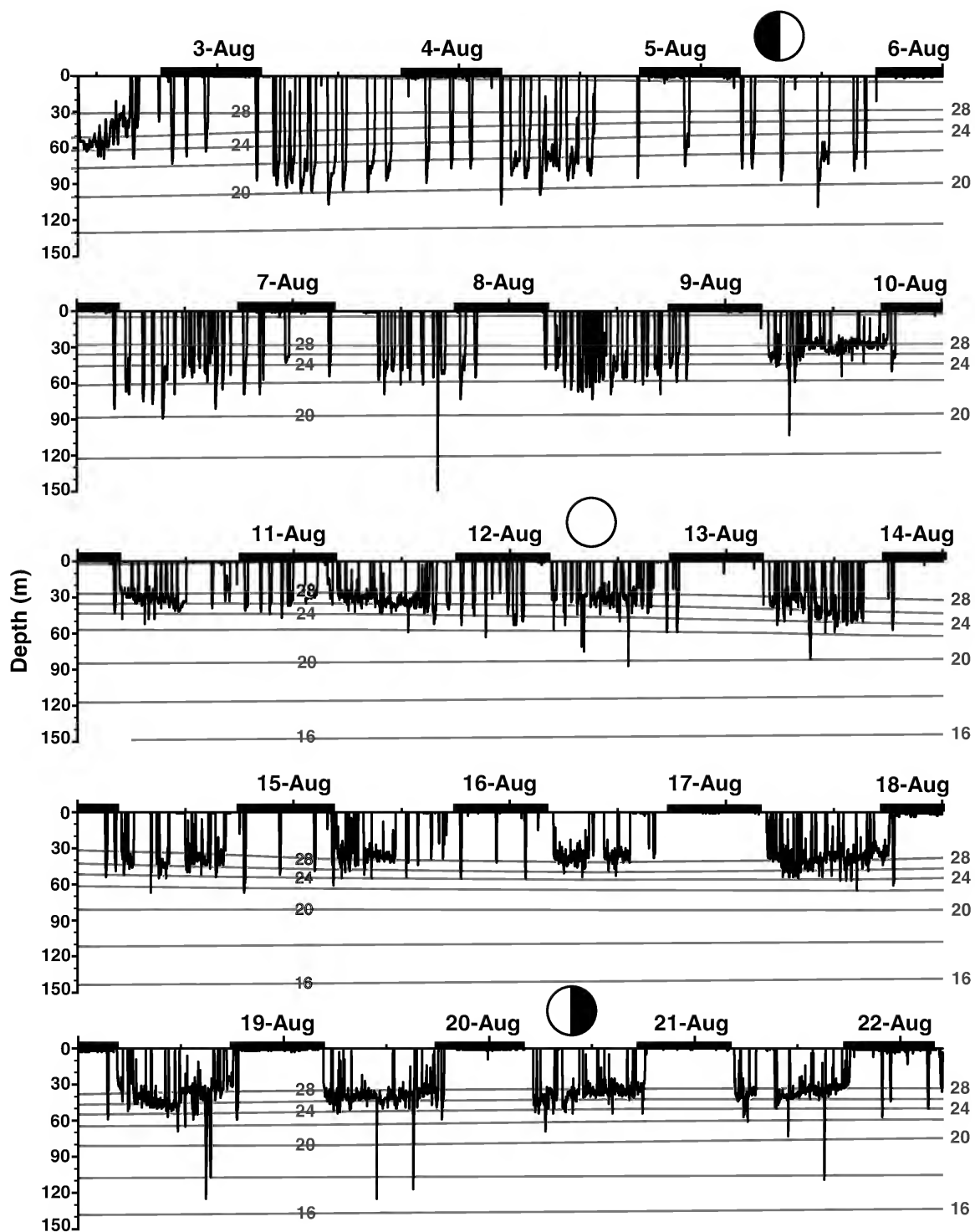


Figure 4. Time series of depth recorded by an electronic tag attached to a blue marlin in the northern Gulf of Mexico during 2004. The deployment, pop-off, and intermediate locations were in the western Gulf of Mexico (west of 90°W longitude). Measurements of depth, temperature and light level were recorded every minute, and the temperature contours were interpolated from the tag data. The black bars on the time axis indicate night, and lunar phase is indicated graphically next to the date. Note that the temperature gradient (in gray) is smoothed and actual temperatures for some of the measurements at the greatest depths are colder than indicated.

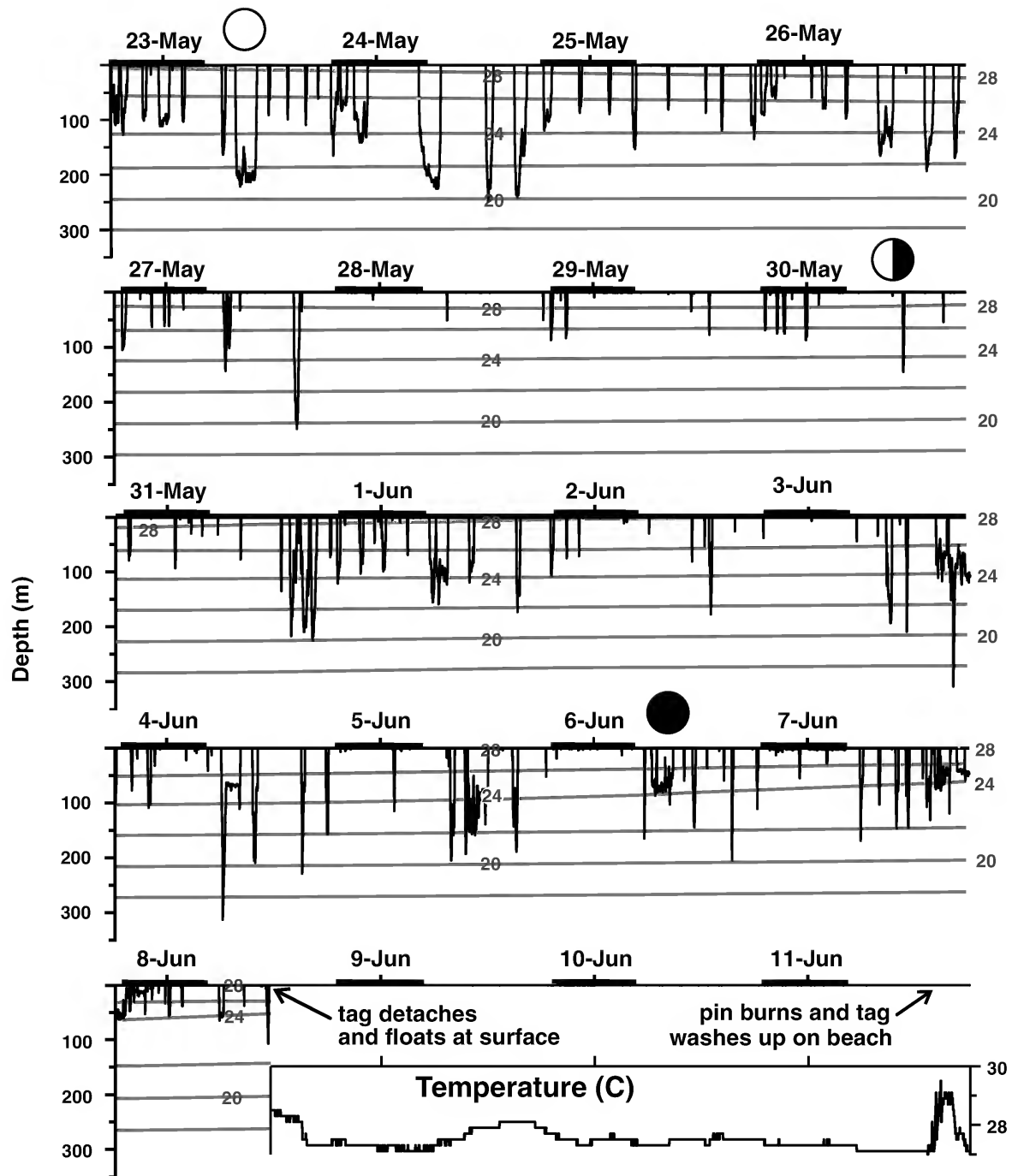


Figure 5. Time series of depth recorded by an electronic tag attached to a blue marlin in the northern Gulf of Mexico during 2005. The deployment, pop-off, and intermediate locations were in the eastern Gulf of Mexico (between 81° and 90°W longitude). Measurements of depth, temperature and light level were recorded every minute, and the temperature contours were interpolated from the tag data. The black bars on the time axis indicate night, and lunar phase is indicated graphically next to the date. Note that the temperature gradient (in gray) is smoothed and actual temperatures for some of the measurements at the greatest depths are colder than indicated.

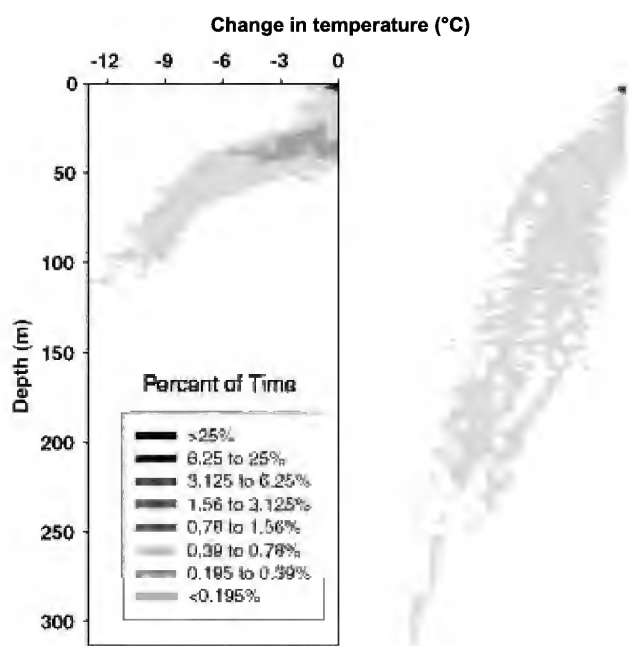


Figure 6. Percent of time as a function of depth and change in temperature relative to the surface (at < 2 m) for 2 blue marlin: one tagged in 2004 in the northwestern Gulf of Mexico (left panel) and one in 2005 in the northeastern Gulf of Mexico (right panel). Areas without any shading represent combinations of depth and temperature change that were not observed, and intervals are inclusive of the upper bound defined in the key.

body size (Brill et al. 1998). In addition, the diving behavior of blue marlin is dependent upon water column structure, and in areas with a well defined shallow thermocline (such as in the western GOM), time-at-depth and time-at-temperature distributions may show additional modes related to time spent in the thermocline. Such bivariate-bimodal patterns are well known from the Pacific (Holland et al. 1990, Block et al. 1992) and the Atlantic (Graves et al. 2002, 2003, Kerstetter et al. 2003), and may vary sharply between day and night with more time at depth during the day. Caution is advised for interpreting diel changes in depth patterns, as distributions of time with depth that pool across days will not be reflective of any particular day. A consistent pattern that varied by lunar phase was equivocal with correspondence to lunar phase in the track from the western GOM in 2004 and no apparent correspondence in the eastern GOM in 2005. Dives to depths >300 m were observed in all three sub-regions and were associated with changes in temperature up to -18°C relative to the surface. Therefore, to address a primary question raised by Goodyear et al. (2003), our results show clearly that the percent of time at any particular depth is not simply a function of the difference in temperature relative to the surface. Instead, it is also dependent upon time of day, lunar phase,

and most importantly the nature of the thermocline, which can vary greatly between sub-regions of the North Atlantic (as demonstrated by the tag data presented here).

Some of the variation in vertical habitat use of the blue marlin in this study can be explained by light level. Blue marlin and other billfish species have specially adapted vision that allows them to forage in low light conditions (Block and Finnerty 1994, Fritsches et al. 2005), thus explaining increased diving behavior at night during a full moon and maximum recorded depths that appear to be independent of temperature change. The greatest depths observed in the PAT tag data represent the limit of light penetration in the GOM, but the maximum depths varied as much as 320 m between individual fish. As the amount of light at depth is dependent upon turbidity and cloud cover, it would be desirable to utilize ancillary meteorological and water quality data to investigate this idea. Yet even with the best available ancillary data, resolution of geolocations from PAT tags is too coarse to match specific tag measurements with environmental conditions, and additional telemetry studies would be necessary. In addition, depths between 300 and 400 m also correspond to the oxygen minimum layer in the GOM (McLellan and Nowland 1963, Morrison et al. 1983); therefore, both low light intensity and limiting oxygen levels (Brill 1994, Prince and Goodyear 2006) likely combine to define the range of depths utilized by Atlantic blue marlin in this study.

It has long been appreciated that habitat standardization of CPUE indices are inadequate due to a paucity of knowledge concerning the behavior of both the longline gear and the fish (Venizelos et al. 2001, Goodyear et al. 2003, Yokawa et al. 2003). The range of diving behaviors of blue marlin that we described here show that more complex models of vertical habitat use (that account for sub-regional differences in water column structure) may improve assessments that rely on longline CPUE indices (see Brill and Lutcavage 2001). Still, it is difficult to determine the position of a longline hook in the water column (e.g., Bigelow 2002, Bigelow et al. 2006), and it may be even more complex to predict the movements and behavior of a large pelagic fish in response to a baited hook. Aspects of fish behavior that relate probability of capture to how the longline gear is set and retrieved have important consequences (Boggs 1992) that cannot be addressed with PAT tags. More importantly, although the time at depths >30 m may represent a very small percentage, it is likely that this part of the habitat has a disproportionately high level of importance as a feeding zone based upon diet analysis for blue marlin (Strasburg 1970, Harvey 1989). Thus, the portion of the habitat in which blue marlin spend the least amount of time may equate to the zone of highest prob-

ability of capture. Although more detailed studies on the behaviors of blue marlin (e.g., Holland et al. 1990) and longline fishing gear (e.g., Boggs 1992) have been short-term and sporadic, there appears to be a great deal of active work that should provide a much improved understanding of the relationship between blue marlin habitat use and catch rates in pelagic longline fisheries in the near future.

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CFRAMP's Large Pelagic Fish Tagging Program

Susan Singh-Renton

CRFM Secretariat, St. Vincent & the Grenadines

John Renton

Girls' High School, St. Vincent & the Grenadines

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CFRAMP'S LARGE PELAGIC FISH TAGGING PROGRAM

Susan Singh-Renton^{1*} and John Renton²

¹CRFM Secretariat, Corea's Building, Halifax Street, St. Vincent & The Grenadines

*Corresponding author. E-mail ssinghrenton@vincysurf.com.

²Science Department, Girls' High School, St. Vincent & The Grenadines.

ABSTRACT CFRAMP's Large Pelagic Fish Tagging Program was established to examine the distribution and movement patterns of *Thunnus atlanticus* (blackfin tuna), *Acanthocybium solandri* (wahoo), *Coryphaena hippurus* (dolphinfish), and *Scomberomorus cavalla* (king mackerel), large pelagic fish species of commercial importance to several Caribbean countries. The Program explored several means to facilitate fish tag and release activities, involving collaborative partnerships with national fisheries administrations, the recreational fishing sector, and individual commercial fishers. A total of 1,143 fish were tagged and released in the coastal waters of several islands within the Eastern Caribbean: 787 blackfin tuna, 250 wahoo, 89 dolphinfish, and 17 king mackerel. To date, only 13 recaptures have been reported. Eleven (11) blackfin tuna, released in the coastal waters of St. Vincent and the Grenadines were recaptured near to, or at original release sites after times at liberty ranging from 5 d to 1,230 d. Similarly, 2 king mackerel, released off the west coast of Trinidad, were recaptured very near original release sites after 74 and 129 d at liberty.

El Programa de Marcado de CFRAMP, para peces pelágicos grandes fue establecido para examinar los patrones de movimiento y distribución de *Thunnus atlanticus* (atún aleta negra), *Acanthocybium solandri* (peto), *Coryphaena hippurus* (dorado común), y *Scomberomorus cavalla* (carite lucio), especies de importancia comercial para varios países del Caribe. El Programa exploró varios medios de facilitar actividades de marcaje y liberación, consistiendo en colaboración conjunta con administraciones de pesquerías nacionales, el sector recreativo, y pescadores comerciales individuales. Un total de 1,143 peces fueron marcados y liberados en las aguas costeras de varias islas localizadas dentro del Caribe del Este: 787 atunes aleta negra, 250 petos, 89 dorado comunes, y 17 carite lucios. Hasta ahora, solo 13 peces han sido recuperados. Once (11) atunes aleta negra, liberados en las aguas costeras de San Vicente y las Granadinas fue recuperado cerca de, o en los puntos de liberación después de varios días en la libertad, entre 5 d hasta 1,230 d. Del mismo modo, 2 peces de carite lucio, liberados en la costa de oeste de Trinidad, fueron recuperados muy cerca de sus puntos originales de liberación después de 74 y 129 d en la libertad.

INTRODUCTION

Various studies have considered the issue of stock identification and distribution of small tuna-like species in the Caribbean (e.g., Constantine 2002, Fable 1990, Oxenford and Hunte 1986a, 1986b). In the Eastern Caribbean, there is evidence that stocks of small tuna-like species and other large pelagic fish species such as dolphinfish are shared based on synchrony in annual abundance trends, and similarity of fishing seasons among neighboring islands (Hunte 1987). The extent of resource sharing among countries of the region has not been quantified. Analyses of size frequency data suggest that the fisheries in this area harvest only a section of the overall fish stocks concerned (George et al. 2001, Parker et al. 2001). Improved understanding of the distributions of these stocks, their movement patterns, and the extent of sharing among fisheries in the region is essential for achieving successful management at the appropriate sub-regional and regional levels.

Fish movement patterns are usually investigated with tagging experiments (e.g., Ortiz 2001). Population parameters such as growth, fishing and natural mortality, and population size can also be derived from tagging data (e.g., Porch 1999, Ortiz et al. 2003). The CARICOM (Caribbean Community)

Fisheries Resource Assessment and Management Program (CFRAMP), which was a co-operative program of 12 Caribbean countries during 1991-1999, established a Large Pelagic Fish Tagging Program to obtain information on the movement patterns and distributions of the stocks of *Thunnus atlanticus* (blackfin tuna), *Acanthocybium solandri* (wahoo), *Coryphaena hippurus* (dolphinfish), and *Scomberomorus cavalla* (king mackerel), large pelagic fish species of regional commercial importance.

MATERIALS AND METHODS

Fish were caught with either rod and reel gear or trolling gear, using artificial bait deployed at depths of ≤ 50 m. For tagging purposes, each fish was usually brought into the boat and placed on its side on a wet mat or sponge. When necessary, the head of the fish was covered with a damp cloth to keep the fish calm. Badly hooked or damaged fish were not used for tagging purposes. Fish were measured for straight fork length (FL), usually to the nearest 0.1 cm, using a commercial tape measure, and weight was estimated using length-weight relationships developed by Battaglia (1993). Each fish was tagged with a single-barb, yellow dart tag used to tag similar pelagic fish

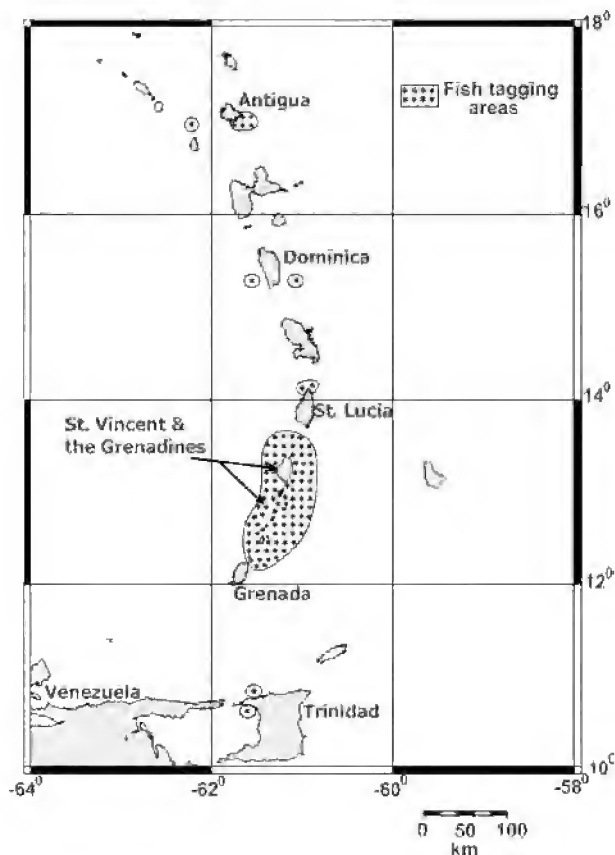


Figure 1. Chart showing island areas in the Eastern Caribbean in which fish tagging activities occurred during the implementation of CFRAMP's Large Pelagic Fish Tagging Program.

species (Fable 1990). After tagging, the fish was quickly returned to the water and observed to ensure that it swam away normally. Any signs of distress were recorded.

During fish tag releases, we recorded tag number, release date, tagger's name, release location, species released, fish size, gender of fish for dolphinfish, fish condition, fish activity upon release, gear and bait used, and depth of fishing. Fish recapture data included tag number, species recaptured, recapture date and location, fish size, gender of fish (if known), fishing gear type, fisher contact details, and data recorder's name. Tag release and recapture data were recorded on data cards, and tag recapture cards were printed in English, Spanish, French, and Portuguese, to facilitate reporting by the range of countries present in and adjacent to the Caribbean region.

We explored several arrangements to facilitate fish tag and release activities. Collaborative partnerships with national fisheries administrations in Dominica, St. Vincent and the Grenadines, and Grenada facilitated tagging during 1-day commercial fishing trips. Fish tagging was also conducted during 3 sportfishing tournaments. A 1-day tournament was held in St. Lucia in May 1997 involving 7

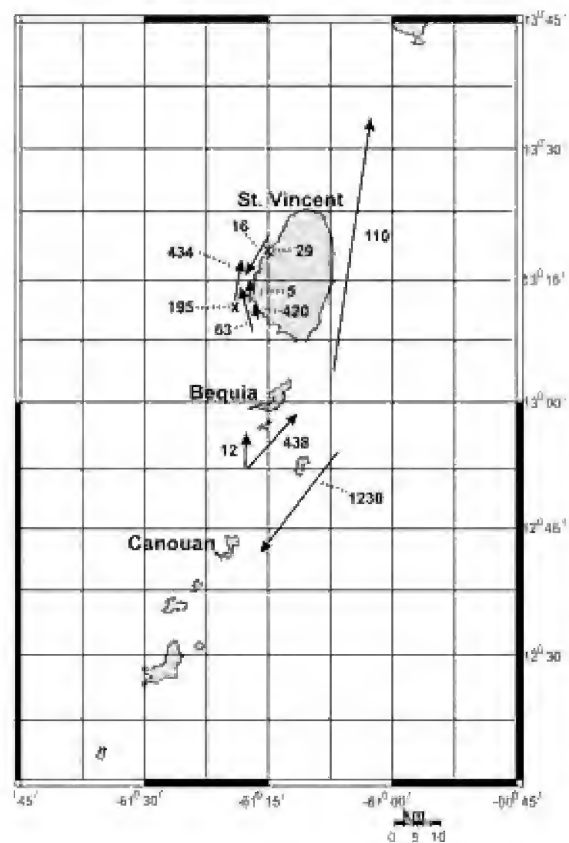


Figure 2. Chart showing the release and recapture positions of 11 blackfin tuna. Each arrow links the release and recapture sites indicating general direction of movement, and the number adjacent to each arrow gives the total number of days at liberty. The symbol 'X' indicates those fish released and recaptured at the same site.

boats. Two 1-day tournaments were held on the Grenadine island of Bequia in July 1996 and July 1997, involving 3 and 7 boats, respectively. Collaborative partnerships with 2 individual commercial fishers in St. Vincent and the Grenadines allowed Tagging Program staff to participate in 1-day commercial fishing trips in this area on a regular basis from March 1997 to June 1999. The commercial fishers received payment for every fish tagged and released, based on the estimated weight. A recreational fisher volunteer program was active during June 1996 to June 1999 and included over 20 volunteers in Antigua and Barbuda, St. Lucia, St. Vincent and the Grenadines and Trinidad and Tobago.

The Tagging Program was advertised using posters, brochures, tee-shirts, and newspaper and television media. A network of tagging correspondents within the Caribbean region was established, and posters were printed in the same 4 languages as tag recapture cards. A cash reward and a Program tee-shirt were offered to fishers for recaptured fish and for providing data.

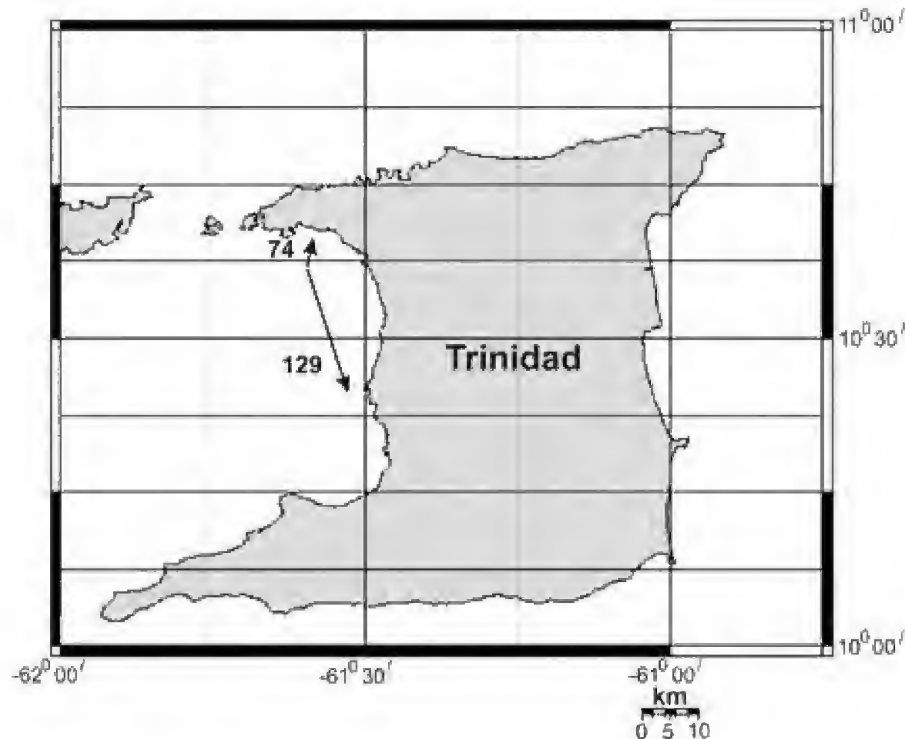


Figure 3. Chart showing the release and recapture locations of 2 king mackerel. Each arrow links the release and recapture sites indicating general direction of movement, and the number adjacent to each arrow gives the total number of days at liberty.

RESULTS AND DISCUSSION

The tagging procedure worked well, and fish were tagged, measured, and released within 30 sec or less, using minimal effort and space. Also, the single-barb dart tags were securely fixed in the observed recaptures, although, the recapture rate for taggers varied notably, with a maximum recapture rate of 22%. Additional studies will be needed to estimate the effects of both tag shedding and tag reporting. The 3 national fisheries administrations completed 9 field trips and tagged and released 35 fish. During the 3 fishing tournaments, 35 fish were tagged and released. Individual recreational fisher volunteers recorded 294 fish tag releases. By far, the most productive, as well as cost-effective, method involved working directly with individual commercial fishers which facilitated 256 fishing trips and 779 fish tag releases.

Most fish tag releases occurred in St. Vincent and the Grenadines (997), with some fish tag releases achieved also in the waters of Antigua and Barbuda (86), Dominica (18), St. Lucia (13), Grenada (15), and Trinidad and Tobago (14) (Figure 1). A total of 1,143 fish were tagged and released: 787 blackfin tuna; 250 wahoo; 89 dolphin-fish; and 17 king mackerel. The variation in number of fish tag releases with species was influenced primarily by market preferences (commercial fishers) and personal taste

preferences (recreational fishers) that favoured the tag and release of blackfin tuna above the other 3 species. Fish tag releases occurred throughout the year, except for king mackerel which were tagged and released during a 1-day recreational fisher volunteer effort in Trinidad and Tobago. The size range of fish tagged and released was 15–89 cm FL for blackfin tuna, 35–130 cm FL for dolphinfish, 50–96 cm FL for king mackerel, and 46–125 cm FL for wahoo.

The rate of tag returns varied among the species. This may have been due to species differences in tag shedding and reporting rates, as well as species differences in survival rate and movement and migration patterns. Reported fish tag recaptures were 11 blackfin tuna and 2 king mackerel. The blackfin tuna were originally released in the coastal waters of St. Vincent and the Grenadines and were recaptured near to, or at, release sites after a time at liberty ranging from 5 to 1,230 d (Figure 2). The 2 king mackerel recaptures also occurred near release sites off the west coast of Trinidad after 74 and 129 d at liberty (Figure 3).

Large pelagic fish, especially tunas, aggregate in areas of upwelling (Ramos and Sangra 1992) and ocean fronts that provide favorable feeding conditions (Fiedler and Bernard 1987). It may be argued that large pelagic fish would take advantage of high prey densities occurring on a local scale, and local occurrence of schools of prey species may attract these migratory fish to stay longer than expected in small sea areas.

When recaptures from different areas of St. Vincent and the Grenadines are compared, the higher number of fish recaptures taken near, or at their release sites along the west coast may be linked to the fact that these are inshore areas. These areas are characterized by tidal currents that interact with a narrow shelf edge and submerged banks to create a local upwelling action that tends to concentrate and attract schools of small prey. These local prey concentrations have the potential to attract predatory fish such as the blackfin tuna on a regular basis for periods of time. In contrast, the 2 blackfin tuna recaptures that were furthest from their release site, had originally been caught, tagged and released off the east coast of St. Vincent and the Grenadines in offshore areas with more oceanic conditions, and where prey might be expected to be more patchily distributed and also more mobile.

In the case of king mackerel, the 2 fish recaptures appeared to have moved only short distances despite one fish being at liberty for 129 d. As with blackfin tuna, these fish were tagged in an area where the tidal currents interact with shoreline features to produce local areas of comparatively high productivity. While food supply and currents may influence residence time, as well as the rate of movement for the king mackerel in this area, other factors such as salinity are thought to affect the movement of king mackerel around the island (Sturm 1978, Sturm et al. 1984). Further studies are needed to confirm the proposed patterns and their causes.

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Patrick McConney

University of the West Indies, Barbados

Hazel A. Oxenford

University of the West Indies, Barbados

Milton Haughton

Caribbean Regional Fisheries Mechanism Secretariat, Belize

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MANAGEMENT IN THE GULF AND CARIBBEAN: MOSAIC OR MELTING POT?

Patrick McConney, Hazel A. Oxenford and Milton Haughton¹

Centre for Resource Management and Environmental Studies (CERMES), University of the West Indies Cave Hill Campus, Barbados, E-mail pmcconney@caribsurf.com

¹*Caribbean Regional Fisheries Mechanism (CRFM) Secretariat, Belize City, Belize, Central America.*

ABSTRACT Does “managing large pelagic fishes” mean the same thing across the diversity of maritime jurisdictions, governance arrangements, economies, languages, cultures, scales of operation and other features of the Gulf and Caribbean region? It would be surprising if it did. Yet international fisheries management urges this mosaic of management to become a melting pot; at least integrated, even if differentiated. This paper examines some themes underlying whether a mosaic or melting pot is the most apt metaphor for where we are, and are headed, in attempts to manage large pelagic fishes in the region. We pay particular attention to the multi-dimensional concept of scale. Included are the scales of management units, fisheries authorities, management outcomes, harvest and postharvest enterprises, and the interdisciplinary perspectives that can be brought to bear on fishery problems and solutions. We are also interested in linkages, because linkage is connected to the scaling-up that is important in a region with many small countries and territories. Even if the management of large pelagics starts as a mosaic, coherent patterns of sub-regional and regional interactions can conceivably be nested and linked to improve the integration, and hence effectiveness, of management interventions ... at least in theory.

RESUMEN Significa “Manejo de grandes peces pelágicos” lo mismo a través de la diversa jurisdicción marina, arreglos de gobernabilidad, economías, lenguajes, culturas, escalas de operación y otras características de la región del Golfo y el Caribe? Sería sorprendente si así fuera. Sin embargo el manejo internacional de pesca sugiere que este mosaico de manejo regional se convierta en un crisol de razas; por lo menos estar integrado, aunque sea de manera diferenciada. Este escrito examina algunos de los temas subyacentes para determinar si mosaico o un crisol de razas es la más apta metáfora para indicar donde estamos, y hacia donde vamos, en nuestro intento por manejar grandes peces pelágicos dentro de la región. Ponemos atención particular al concepto multi-dimensional de “escala”. Incluidas están las escalas de unidades de manejo, autoridades de pesca, resultados de manejo, empresas para cosecha y post cosecha las de perspectivas disciplinarias e inter disciplinarias que puedan aplicarse a los problemas y soluciones de la pesca. Estamos igualmente interesados en enlaces, ya que el enlace está conectado al aumento a escala que resulta importante dentro de una región con muchos pequeños países y territorios. Aunque el manejo de grandes pelágicos empiece como un mosaico, patrones coherentes de interacciones sub-regionales y regionales pueden concebiblemente anidarse y enlazarse a fin de mejorar la integración, y por ende la efectividad, de intervenciones de manejo... por lo menos en teoría.

INTRODUCTION

Wedge between the continental Americas, the Gulf of Mexico (GOM) and Caribbean Sea contains more than 100 million people located in over 30 countries and territories, the majority of which are islands. It would be surprising if “managing large pelagic fishes” meant the same thing across the diversity of maritime jurisdictions, governance arrangements, economies, languages, cultures, scales of operation and other features that reflect the heterogeneity of the GOM and Caribbean Sea. Yet international fisheries management trends urge this diverse mosaic to become a melting pot; at least integrated in its management regimes, even if differentiated to some extent.

For example, the International Commission for the Conservation of Atlantic Tunas (ICCAT) recommended management measures for large pelagic fishes are typically intended to be uniformly applied in the area. Some countries in alliances such as the Organization of Eastern Caribbean States (OECS) and the Caribbean Community

(CARICOM) have harmonized their national fisheries regulations for demersal inshore and turtle species, and may yet do so for large pelagics. Major importing countries insist that their Caribbean suppliers meet international fish trade and quality standards (e.g., Hazard Analysis Critical Control Point systems, European Union Import Standards for Fish Products) that extend backwards along the fish chain to small-scale harvest operations. However, despite these forces of homogenization, there are other factors that maintain heterogeneity and reinforce the differences in the fisheries and fisheries management regimes of the region.

These differences include the sizes and capacities of the fisheries management authorities, the scales of the industry components (vessels, landing facilities, processing plants, etc.), the relative size and value of the commercial harvest, the values of recreational fisheries, the institutional and governance relationships among resource users or other stakeholders and managers, the capabilities of fisheries research agencies, and more. The differences

are reflected in the approaches to fisheries management, the inputs and outcomes, and they apply to all parts of the fish chain in both private and public enterprise.

In the management of large pelagic fishes in the region there will always be pros and cons as to whether complete uniformity (extreme melting pot) is more desirable than high diversity (extreme mosaic) or the reverse, or some middle ground. The conclusion will often be situation (fishery, management measure, country, stakeholder, etc.) specific. Leveling the playing field through standardization (from reporting procedures to technical regulations) may be equitable under some circumstances, but be highly inequitable in others where the capacity to manage differs significantly among fishery participants. However, regardless of whether or not industry and management diversity is considered “good” or “bad,” fisheries managers and other stakeholders should be aware of what factors maintain or erode diversity to greater and lesser extents. Without this knowledge it will be difficult to engineer any planned degree of integration which is an important ingredient in maintaining the mosaic without much mixing or stirring the melting pot to achieve the best blend.

This paper examines some of the themes underlying whether “mosaic” or “melting pot” is the most apt metaphor for where we are, and are headed, in attempts to manage large pelagic fishes in the region through various means of integration. We pay particular attention to the multi-dimensional concept of scale because it is pervasive in the region. We are also interested in linkages through networks, because linkage determines whether or not scaling-up is feasible. The scaling up of management can be desirable in a region with many small developing countries and territories that rely heavily on project-implemented fisheries management. Following the introduction of what we mean by scale and network, these concepts are applied in some brief analyses of fisheries in the GOM and Caribbean Sea region. We attempt to provide unconventional and provocative perspectives on these topics, to see how well the metaphors fit the situations and to draw some conclusions from the findings.

Scale and Network Concepts

The concepts of scale and networks, for the purpose of this discussion, are best addressed in the context of fisheries governance as a complex adaptive system (CAS) and social-ecological system (SES) (Garcia et al. 2003, Bavinck et al. 2005, Kooiman et al. 2005, Wilson 2006). CAS are highly interactive internally, and often exhibit the capacity to self-organize and adapt without outside influence (Mahon 2005). SES are conceptualized as being far more intricately interwoven than is achieved by simply

fitting humans into ecosystem models or adding natural resource dynamics to models of human society. The SES view emphasizes that social and ecological systems are inevitably linked and integrated, and that the delineation between the 2 systems is artificial and arbitrary (Berkes and Folke 1998, Anderies et al. 2006).

Scale is a concept common to most disciplines. SES operate at multiple scales so it is critical to consider the scale or range of scales at which we can collect and process information, reach conclusions on and manage effectively; ecological scales are both spatial and temporal. Social scales also include the jurisdictional and institutional, among others. Integrated into an SES perspective, complex and dynamic interactions and feedback loops may occur within or across ecological and social scales (Cumming et al. 2006).

Using the scheme of Cash et al. (2006), “scale” is the overall label of the feature being measured such as spatial, temporal, jurisdictional, institutional, management arrangements, network, and ecological knowledge scales. “Level” is the particular resolution within a scale. “Multi-scale” means more than one scale, and “cross-scale” signifies interactions across them. “Cross-level” refers to interactions among different levels within the same scale (Figure 1).

In Figure 1, considering a hypothetical Caribbean fisheries example, one may have an international fisheries instrument with international jurisdiction (such as the FAO Code of Conduct for Responsible Fisheries) that drives fisheries policy at the sub-regional (e.g., eastern Caribbean) and country (e.g., St. Vincent and the Grenadines) levels. This is multi-scale, cross-scale and multi-level. The international instrument also drives policy at the national jurisdictional level (cross-level). In this example, because of vessel flagging practices, national jurisdiction may extend well beyond the geographic borders of the country. All of the above may be top-down (shown by descending unidirectional arrows), but at lower levels in this multi-scale case there are two-way interactions between watershed and settlement as fisheries is integrated into coastal management according to the FAO Code. There are also organizational interactions such as of the Fisheries Division with communities (e.g., village council jurisdiction) and individuals (who have personal social networks) for getting the Code implemented.

Three common “scale challenges” include: the failure to recognize important scale and level interactions altogether (ignorance); persistence of mismatches between levels and scales (mis-match); and failure to recognize heterogeneity in the way that scales are perceived and valued by different actors (plurality)(Cash et al. 2006). In natural

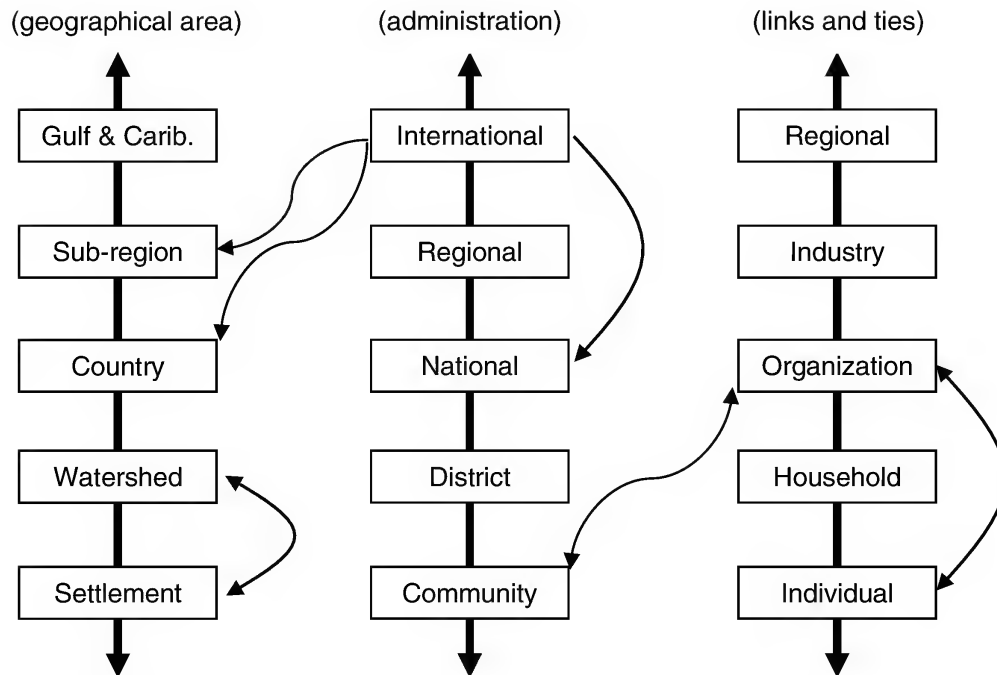


Figure 1. Spatial, jurisdictional and network multi-level scales showing cross-scale and cross-level linkages (Based on Cash et al. 2006). Single headed arrows indicate unidirectional action (such as top-down influence) while double headed arrows indicate two-way interaction (such as negotiation).

resource management systems, social-ecological scale mismatches are evidenced by losses of adaptive capacity and resilience (Cumming et al. 2006). Successful co-management institutions provide examples of approaches to scales and linkages that address cross-scale governance issues (Berkes 2002, 2006). This brings us to networks.

In the context of this paper, network analysis focuses on the interactions between SES components and the ways in which the structure of nodes and links, and the flows contained within, affects the performance of the system on a variety of scales at various levels. Network analysis has been applied to both social systems and ecological systems, combining qualitative and quantitative information, but seldom integrating SES (but see Janssen et al. 2006). Network architecture or structure is of little value unless the nature of flows through the network and its purpose are also known. For example, a dense network may be good for the rapid diffusion of a beneficial innovation or information, but it may also spread irresponsible fishing methods or constrain individual fisheries managers from experimentation for adaptation if close-knit cliques are formed.

Depending on the type of analysis (food web, community, fishery, business) network nodes can be individuals, organizations, countries or whatever entities are appropriate. The focus on ties (relations between the focal node and

other nodes) and links (relations only between other nodes in the focal node's network) as the main features that confer network properties, rather than the nodes themselves, is distinctive to network analysis. Ties and links between nodes may be characterized in innumerable ways. In social network analysis the strengths and directions of the flows of information, assistance, funds, conflict and other types of exchanges are quantified and described. Although networks are often illustrated 2-dimensionally as flat structures, adding a third dimension or height can display differences in levels within a scale, disparities in power and other variations which may be perceived as inequitable or otherwise problematic, and hence attract management attention (Figure 2).

Figure 2 depicts a hypothetical personal social network with a longline captain (LLC) as the focal node. His network contains his crew (LLF), the boat owner (BO) and fisheries officials of various ranks. The most powerful of the latter is the Chief Fisheries Officer (CFO) with whom there is only a top-down relationship. Communication with the CFO requires the captain to go through his boat owner and a fisherfolk leader (FFL), or he can speak to one of the lower ranked fisheries officials (DC or SFO). Typically, hierarchical public administration is illustrated by the links between the fisheries officials. We now turn to how scale, linkage and network concepts are applicable

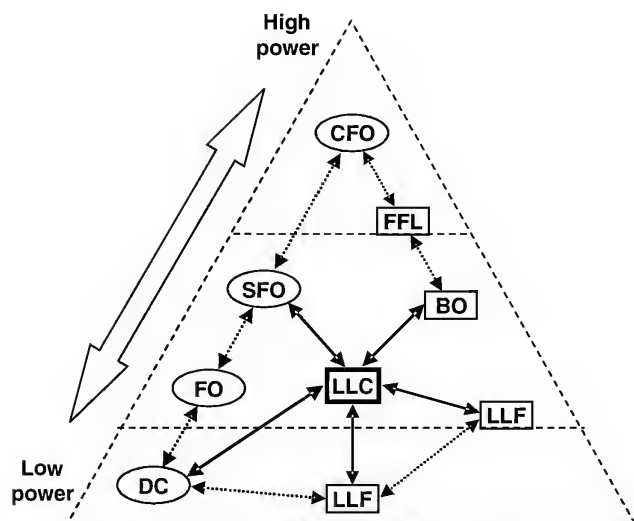


Figure 2. Network of fishery stakeholders with power level hierarchy superimposed CFO = Chief Fisheries Officer; SFO = Senior Fisheries Officer; FO = Fisheries Officer; DC = Data Collector; FFL = Fisherfolk leader; BO = boat owner; LLC = longline captain (the network node here); LLF = longline fisher. Arrows denote communication with direction(s) indicated, solid for ties and dotted for links. Dashed lines in triangle define three different levels of power. State stakeholders are shown as oval shapes and industry stakeholders in rectangular boxes.

to the management of large pelagic fishes in the GOM and Caribbean.

Fisheries perspectives

In the GOM and Caribbean, large pelagic fishes are the targets and by-catch of commercial, recreational and subsistence fisheries that range from large scale to very small scale. The species and species groups we refer to are primarily the large tunas, billfishes, swordfish, dolphinfish, wahoo and large mackerels. Sharks are often included as by-catch. The most recent information on the status of stocks and fishery assessments is from ICCAT (www.iccat.int). However, although stock status, fishery trends and regulatory measures are clearly pertinent to management, they are not the main focus of this paper. Instead, we examine some of the practical consequences that scale, linkage and integration have for management, by means of brief examples mainly from a CARICOM perspective.

The mosaic aspects of wider Caribbean geography are conspicuous in the illustration of marine jurisdictions comprising hypothetical Exclusive Economic Zones (EEZs) based on the principle of equidistance (Figure 3). This jurisdictional mosaic consists of 26 countries and the 19 dependent territories of 4 other countries; the majority of these countries and territories are small island developing states (SIDS) with high dependence on fishing and

tourism. There is considerable spatial and seasonal heterogeneity in marine productivity and oceanographic features (Mahon 2002). In terms of ecological linkages, the trophic connections between productive coastal areas and less productive offshore planktonic or pelagic systems are poorly understood for this region. Food chain linkages between exploited resources with differing scales of distribution and migration through the EEZs or across the high seas, such as flyingfish and large pelagics, have not received much consideration in management. However, supporting research is currently in progress. Knowing such linkages may be critical to preventing the stock depletion that has occurred in many other areas and systems where predator-prey relationships have not been adequately considered in the exploitation of large pelagic species (Mahon 2005).

A second, but patchier, mosaic layer superimposed on these EEZs comprises the various organizations and alliances to which the countries and territories in the region belong. The spatial scales of the organizations can be illustrated by highlighting their membership. This is also shown in Figure 3 for CARICOM countries, but there are several other organizations relevant to large pelagic fisheries including the Western Central Atlantic Fishery Commission (WECAFC) of the Food and Agriculture Organization (FAO), OECS and Organización del Sector Pesquero y Acuicola del Istmo Centroamericano (OSPESCA) among others (Chakalall et al. 1998, 2007).

It is immediately obvious that this patchwork of marine jurisdictions and organizations poses serious challenges to the integration of fisheries management in the region, and especially so in the case of large pelagics that range beyond the region (Singh-Renton et al. 2003). Spatial (ecological) and jurisdictional (management) scales are generally not well matched at any level, and this is well known (Mahon and McConney 2004a). However, little attention has been paid to the lower levels on the spatial and jurisdictional scales and how these are linked to the higher levels. An exception is the analysis by Berkes (2006) of tuna management in the eastern Caribbean within the context of cross-scale governance (Figure 4). He argued that international, regional, national and community levels are mis-matched and poorly linked. He goes on to point out that this is also true for the scales of power and knowledge seldom considered in management.

Using the case of small-scale fishers in Gouyave, Grenada, it has been shown that their local fishery knowledge has no way of making an impression on the complex science used in ICCAT assessments (Grant and Berkes 2004, Grant and Rennie 2005). ICCAT wields immense power that affects the livelihoods of artisanal longline fishers and constrains their opportunities. The impacts of

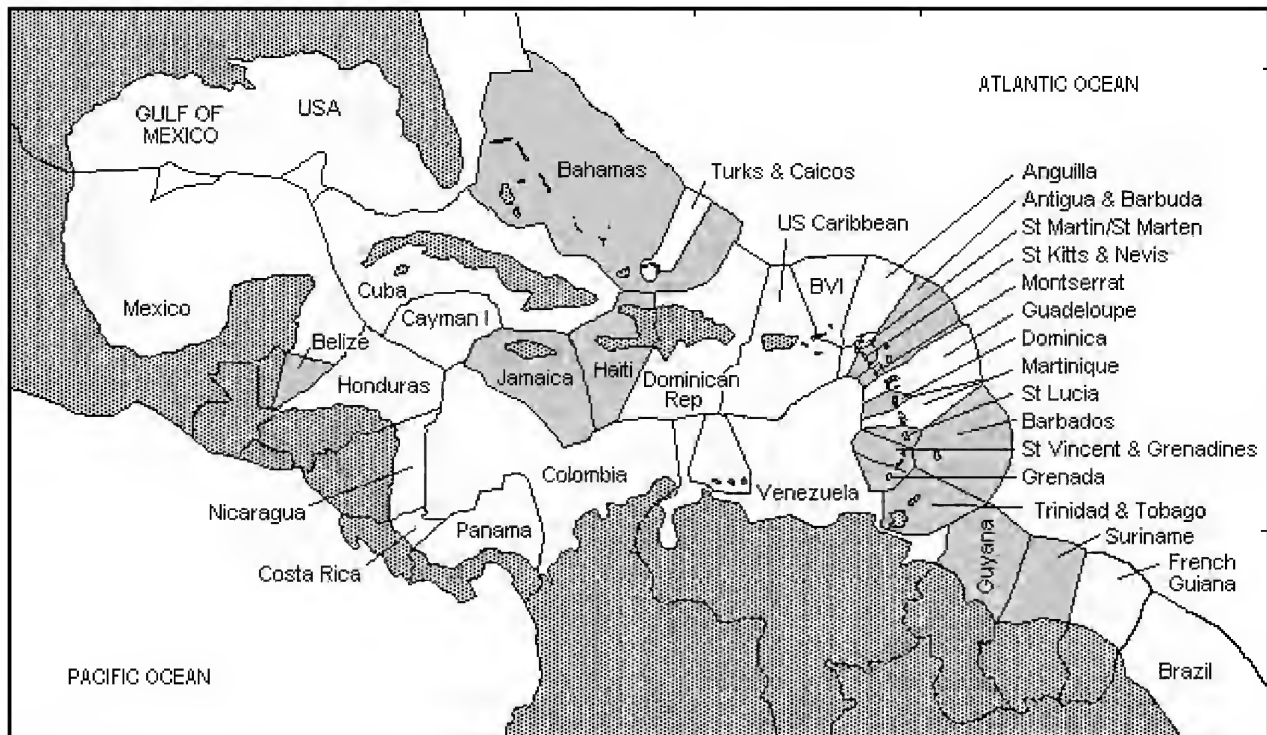


Figure 3. The wider Caribbean region highlighting hypothetical EEZs of CARICOM countries (Adapted from Haughton et al. 2004).

ICCAT allocation criteria and management measures at the community level are not well documented in a form that is likely to be consumed by the international Commission even if socio-economic matters were to be given more consideration. Indeed, even at the regional level of CARICOM, there is little that has been done by Member States to comprehensively document the socio-economic, institutional and linkage aspects of their fisheries. A study to examine these aspects has only recently been undertaken in the context of establishing a Common Fisheries Policy and Regime (Phillips et al. 2006). However, much more needs to be done to integrate livelihood perspectives into the management of large pelagics if small fishing communities are to be integrated into management.

The above analysis argues for bottom-up integration in fisheries management, but it would be erroneous to assume that information on international or regional fisheries management routinely penetrates beyond the national level to reach fishing communities, fisher organizations and individual fishers. While fisheries managers in the region may well speak and understand the language of ICCAT or other international fisheries bodies such as the bodies of FAO, this is not the case for fisherfolk. A barrier to top-down integration and sharing of fisheries management outlooks often exists at the national level due to the limited extension and outreach capacities of small fisheries authorities. Local level fisherfolk are typically unaware of the scale

mis-matches and lack of integration since ICCAT and the concepts of managing large pelagics are completely alien to them. National barriers to integration and scaling up are perhaps the most persistent.

In considering the issue of capacity, Mahon and McConney (2004b) argue that fisheries authorities in small island developing states (SIDS) cannot simply be scaled up to perform as miniatures of the large and relatively well funded agencies of developed countries such as the federal National Marine Fisheries Service (NMFS) and the state authorities in the United States of America. These authors observe that technical capacity to manage fisheries will almost always be below optimum, and suggest that it be supplemented by more people-centered approaches. In the case of Barbados, the fisheries authority set out, as advice to policy-makers, the costs and benefits of becoming an ICCAT Contracting Party prior to the country becoming a member. In this policy proposal, the costs included recruiting an additional fisheries officer to join the single fisheries biologist primarily responsible for all science associated with the country's nine fisheries management plans. Although the policy decision was to join ICCAT, the additional officer was not approved. The main justification for the additional officer was to bridge the gap between the regional and international levels and the local fishing industry. The intent was to "translate," in real time, ICCAT communications so that the local longline industry would

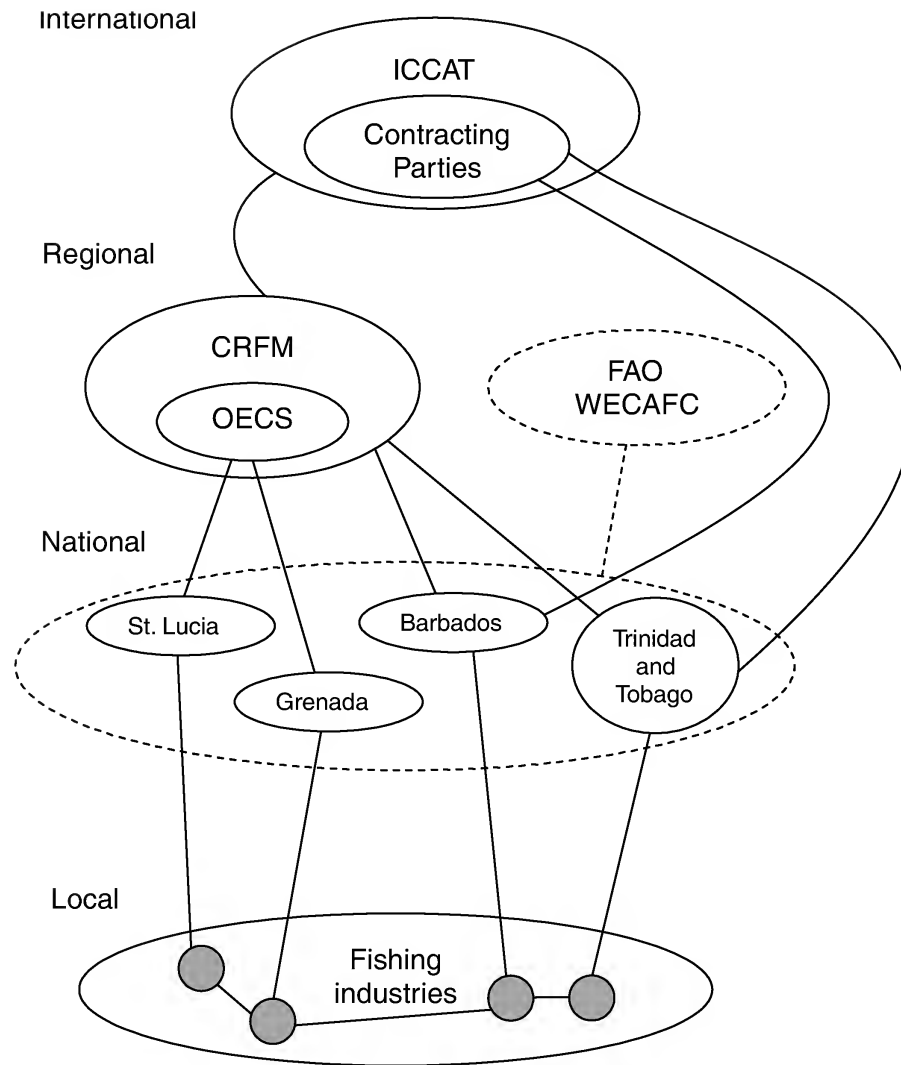


Figure 4. Cross-scale networked governance in Caribbean tuna management. ICCAT=International Commission for the Conservation of Atlantic Tuna, CRFM=Caribbean Regional Fisheries Mechanism, OECS=Organization of Eastern Caribbean States, FAO=Food and Agricultural Organization of the United Nations, WECAFC=Western Central Atlantic Fisheries Commission (Adapted from Berkes 2006). Dashed lines of FAO WECAFC and around its member states indicates relationships of secondary importance. Dark-filled fishing industry circles represent dense networks of non-State stakeholders

gain a much better appreciation of how large pelagic fishes are managed, or not managed, and make meaningful inputs into the Barbados perspective and policy on management. Although all cannot be blamed on the absence of a single officer, the very limited capacity of the fisheries authority to engage the industry has severely constrained integration at national and higher levels.

For a fuller explanation of constraints on integration at the national level we also need to look beyond the management authority and examine the linkages to policy decision-making and to fisherfolk collective action as interest or pressure groups. Policy-making and constituent lobbying are closely related in political processes. Although large pelagic fisheries are currently or potentially impor-

tant to the societies and economies of most CARICOM countries (Mahon and McConney 2004a), these fisheries seem to be of limited political interest and do not attract the attention of ministers responsible for fisheries. Again taking Barbados as an example, large pelagics dominate foreign exchange earnings from fisheries through export of tunas and swordfish. The scale of fishing is small, but larger than what was described above for Grenada. Yet few linkages exist between the industry and fisheries authority that assist in empowering the latter successfully to pursue policy decisions and to build management capacity to participate more effectively in ICCAT. Because the industry shows no interest in ICCAT, and because large pelagics are not very prominent icons in local fisheries culture,

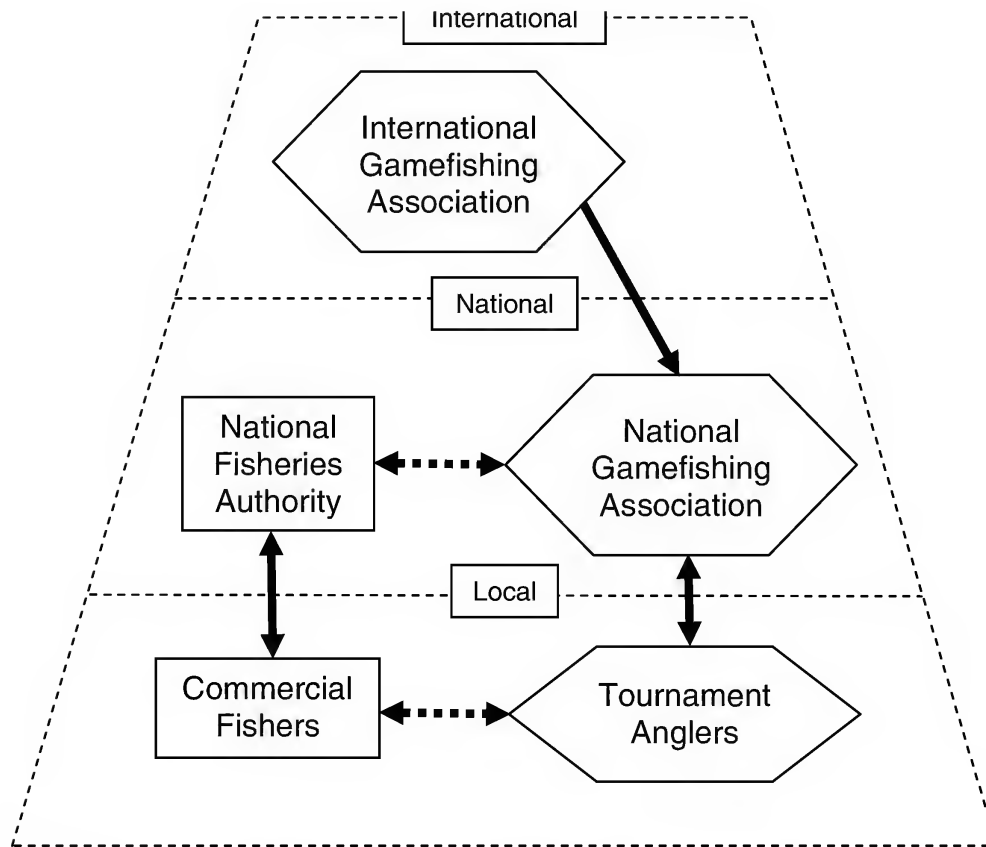


Figure 5. Strengths and weaknesses of linkages in recreational fishing at three levels on the jurisdictional scale. Solid arrows are strong linkages, dotted arrows are weak linkages. Directions are indicated by arrow heads. Recreational fishery stakeholders are shown as hexagons, and commercial fishery stakeholders as rectangles.

the Fisheries Division is unlikely to be able to attend its meetings or to obtain annual budgetary allocations for improving research or management. This contrasts sharply with the fisheries for flyingfish and sea urchins in which cultural and popular aspects are prominent and these fisheries receive a considerable amount of attention from policy decision-makers. The lesson here is not to underestimate the importance of local politics, power and culture in fisheries management. If managers wish large pelagics to attract the attention of policy-makers to management issues, they may have to focus first on increasing interest among their constituents.

These constituents include fisherfolk organizations that are typically too weak and poorly organized to act collectively as interest or pressure groups, resulting in dependence on a few key individuals. Such persons may be involved in the harvest, processing, marketing, distribution and trade of large pelagics. Some may be members of fisherfolk organizations such as associations and cooperatives, but in CARICOM countries most of these groups are rooted in the harvest rather than postharvest sector. Significant

proportions of the large pelagics landed in most countries are purchased and exported by private or public sector companies that tend to be individualistic rather than integrated in a postharvest organization. Also, as the scale and capital investment of fishing enterprises increase, non-fishing vessel owners may be less inclined to be in fisherfolk organizations since wealth is often accompanied by power and socio-economic status. As such, their individual interests can be met without organizational affiliation. Hence collaborative relationships are likely to be much stronger among fisher captains and crew than among boat owners and persons in postharvest. Social networks are often important assets in coping with the uncertainties of fishing even more than formal organizations are (McConney 1997). Therefore, strategically, fisheries authorities should aim to link with influential fishers of large pelagics in order to pass on communications concerning the management of the industry. If social networks are dense, then the diffusion of information can be fast and extensive with these captains acting as nodes. If fisheries authorities have an appreciation of social network structure, and the

flows within them, it is possible for them to be used instrumentally in fisheries management to increase the degree of integration. Longline fishers are known to have trans-boundary networks for information exchange and assistance at sea that span much of the south-eastern Caribbean (A. Kinch, Barbados longline fisher, pers. comm.). These informal fisher networks are likely to be more efficient for transmitting information than any official national or regional system of communication.

The recent initiative of CARICOM leaders to strengthen and deepen regional integration by establishing a single market and economy to replace the common market may have significant implications for the management of large pelgics and other shared species. The intentions of this initiative are to: 1) fully integrate and liberalize the internal markets and economies of CARICOM States to facilitate the structured integration of production of goods and services; 2) facilitate the unrestricted movement of capital, labour and technology; and 3) allow access by nationals to the collective resources of the region on a non-discriminatory basis (CARICOM 2002). The common fisheries policy being developed as part of this process is designed to give effect to these general objectives while ensuring effective conservation and management of the fisheries resources.

Another related integration initiative that may become relevant to the management of large pelagics is the CRFM's project to strengthen and link local and national fisherfolk organizations into a regionally networked system. If this initiative is successful, it may be more feasible for fisherfolk organizations to participate in fisheries management through the bodies of the CRFM such as the Caribbean Fisheries Forum that addresses policy advice and the Large Pelagics Working Group (LPWG) that was set up in 2000 to conduct and contribute to fishery assessments. To date the LPWG has functioned as a loose network mainly of individuals who are responsible for data management in national fisheries authorities and who share information just prior to the CRFM science meetings in order to determine and report on fishery and resource trends. These assessments have been assisted by scientists from outside the region (UK and USA) thereby creating brief additional linkages. A weakness in the LPWG networking is, however, that the inter-sessional activities, linkages and communications are not well developed; a constraint related again to the limited capacities of both the CRFM Secretariat and its Member State fisheries authorities. This working group is in urgent need of strengthening if the CRFM is to have a stronger presence at ICCAT and if it aspires to becoming the regional fisheries management organization for the pelagic species that are not of great immediate interest to

ICCAT (e.g., dolphinfish, wahoo, blackfin tuna), perhaps under some type of inter-agency cooperation agreement.

In the management of the postharvest sector, the small-scale fishing industries have learned about ICCAT through some of the trade requirements such as swordfish certificates of eligibility to reduce the harvest, or at least the landing and export, of undersized fish. Many fishers in the eastern Caribbean are also aware of the trade and conservation issues associated with bluefin tuna that complicate their rare incidental catches of these prized animals. It is possible that more is known about the conservation and management of large pelagics through the practice of trade than through the dissemination of information on harvest regulations such as size limits and quotas. In the case of trade, the US market and that country's adherence to ICCAT management measures have tended to integrate management across exporting countries through business networks.

Caribbean commercial fishers are becoming increasingly knowledgeable about the rules and restrictions governing recreational fishing, and are aware of how recreational lobbyists have reduced or excluded commercial harvests in some places and fisheries in the USA. For anglers, many gamefishing clubs will be made aware by an organization such as the International Game Fish Association (IGFA) of current responsible fishing practices such as tag and release and size limits (Antia et al. 2000). Tournament anglers travel to fish under the rules in other countries more often than commercial fishers since there are no access agreements covering large pelagics in the CARICOM region. From a network perspective there are strong connections among anglers as a community of interest. The connections between the gamefishing bodies and national fisheries authorities, and between anglers and commercial fishers, are likely to be fewer and weaker (Figure 5).

This network information is pertinent to initiatives such as that of The Billfish Foundation to improve conservation in the region. Knowing the linkages facilitates directing effort and information to where success is most likely.

Of mosaics and melting pots

The brief analysis presented here strongly suggests that large pelagics require more attention from fisheries managers in the region, but the managers also need new tools and perspectives to improve their chances of successful management. The mosaic metaphor sets a scenario in which the entities are poorly connected or integrated and attempts to scale up will be confronted by many boundaries and barriers. The melting pot suggests strong

integration while maintaining some differentiation or recognizable diversity with few obstacles to scaling up. In the GOM and Caribbean the management of large pelagic fishes is extremely weak and is still mostly a mosaic (little integration) with some areas that are melting pots (stronger integration) such as among OECS and CARICOM Member States.

Informal linkages among fishers and linkages related to fish trade or recreational fisheries seem to be better developed than more formal linkages among management bodies and between them and either policy-makers or fisherfolk. A critical area for future management research could be the characterization of fisher social networks. Regarding the "scale challenges," in the GOM and Caribbean, there is little ignorance about issues of scale, but there are scale mis-matches and plurality issues. These need to be urgently addressed if the management of large pelagic fishes is to be improved, integrated and scaled up where possible.

Not all aspects of these problems can be tackled simultaneously. It is necessary to identify critical areas for integration and determine what needs to be scaled up since fisheries authorities will remain constrained by limited capacity in relation to their areas of responsibility, at least in CARICOM countries. Use of complex adaptive systems concepts such as scale and networks in interdisciplinary fisheries research guided by social-ecological systems perspectives will help to create new views for fishery managers. Managers and researchers need to draw more upon emerging social science and management theory to address the human dimensions of management and to deal with the pervasiveness of constraining power dynamics and conflict in the management of large pelagic fishes.

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Sandra C. Grant
University of Manitoba

Fikret Berkes
University of Manitoba

John Brierley
University of Manitoba

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UNDERSTANDING THE LOCAL LIVELIHOOD SYSTEM IN RESOURCE MANAGEMENT: THE PELAGIC LONGLINE FISHERY IN GOUYAVE, GRENADA

Sandra C. Grant^{1*}, Fikret Berkes¹, and John Brierley²

¹Natural Resources Institute, University of Manitoba, 70 Dysart Road, Winnipeg, Manitoba, R3T 2N2 Canada, Phone (204) 474-8873, Fax (204) 261-0038. *E-mail linegrant@gmail.com

²Department of Environment and Geography, University of Manitoba, 211 Isbister Building, University of Manitoba, Winnipeg, Manitoba, Canada R3T 2N2

ABSTRACT There is a need to include social objectives in fisheries management, and this paper focuses on one set of social considerations, those regarding livelihood. We pay particular attention to sustainable livelihood strategies, the importance of commercial pelagic longline fishing for the entire community livelihood system, and implications for management. Field data were obtained between December 2002 and March 2004 in Gouyave, Grenada, using participant observation, semi-structured interviews, and a quantitative survey. The economic base (fishing and agriculture) of the community is both unpredictable and seasonal, therefore individuals and households engage in diverse strategies to secure their livelihood. Three livelihood strategies were deemed important: 1) livelihood diversification, developing additional sources of income from agriculture, wage labor, and trade work, 2) fishing diversification, learning to switch to alternative gear and species, and 3) the availability of an informal “social security net” involving cash and in-kind assistance. These strategies help to spread the flow of income and food during lean times and across seasons. A major management implication is that fishery managers need to pay attention to the multi-species nature of fisheries and to the importance of livelihood diversification, including reliance on other economic sectors.

RESUMEN Existe la necesidad de incluir objetivos sociales en el manejo de la industria pesquera y este artículo se focaliza en un grupo de consideraciones sociales, las que se refieren al sustento. Prestamos particular atención a las estrategias de los sustento sostenibles, la importancia de la pesca pelágica comercial para el sustento de toda la comunidad y las implicaciones para su manejo. Los datos de campo fueron obtenidos entre Diciembre del 2002 y Marzo del 2004 de Gouyave, Grenada a través del estudio de los participantes, entrevistas semi-estructuradas y un examen cuantitativo. La base económica (pesca y agricultura) de la comunidad es tanto impredecible como variable, por lo tanto individuos y hogares adoptan estrategias diversificadas para lograr la seguridad del sustento. Tres estrategias de sustento fueron consideradas importantes: 1) diversificación de las actividades para sustento desarrollando fuentes de ingresos adicionales en agricultura, labor pagada y trabajo de obrero, 2) la diversificación de la pesca aprendiendo a utilizar hacia equipos y especies alternativas, y 3) la disponibilidad de una red de seguridad social que incluye asistencia monetaria y en especie. Estas estrategias diversificadas ayudan a distribuir el flujo de ingresos y alimentos a través de las estaciones. Un mayor involucramiento en el manejo implica que los gerentes pesqueros presten mayor cuidado a la naturaleza multi-especies de la pesca y a la importancia de la diversificación del sustento, incluyendo la confianza en otros sectores económicos.

INTRODUCTION

Caribbean fishery managers, as elsewhere, generally use biological and economic objectives to manage fisheries. The need to include social objectives has been discussed, but more needs to be done to integrate this consideration into fisheries planning and management (Berkes et al. 2001). Social objectives allow for the inclusion of human dimensions (resource user, community, and the socioeconomic environment) in the fisheries management system. One way to include social objectives is to analyze how individuals and households make a living from fishing but also how they structure their livelihood system, including non-fishing activities.

A livelihood “comprises the assets (natural, physical, human, financial and social capital), the activities, and

the access to these (mediated by institutions and social relations) that together determine the living gained by the individual or household” (Ellis 2000, p.10). A large literature deals with frameworks of assets and vulnerabilities (Bebbington 1999). A sustainable livelihood is one with the ability to cope with and recover from stresses and shocks, maintain or enhance its capabilities, assets, and entitlements, while not undermining the natural resource base (Chambers and Conway 1992). A Caribbean household consists of people who may or may not be related by kinship, but who share living space including a kitchen and certain budgetary items such as food and rent. Hence, a household can be a single person living alone or a group of friends living together (Barrow 1998).

The concept of sustainable livelihood is useful for understanding the complexity and diversity of making a

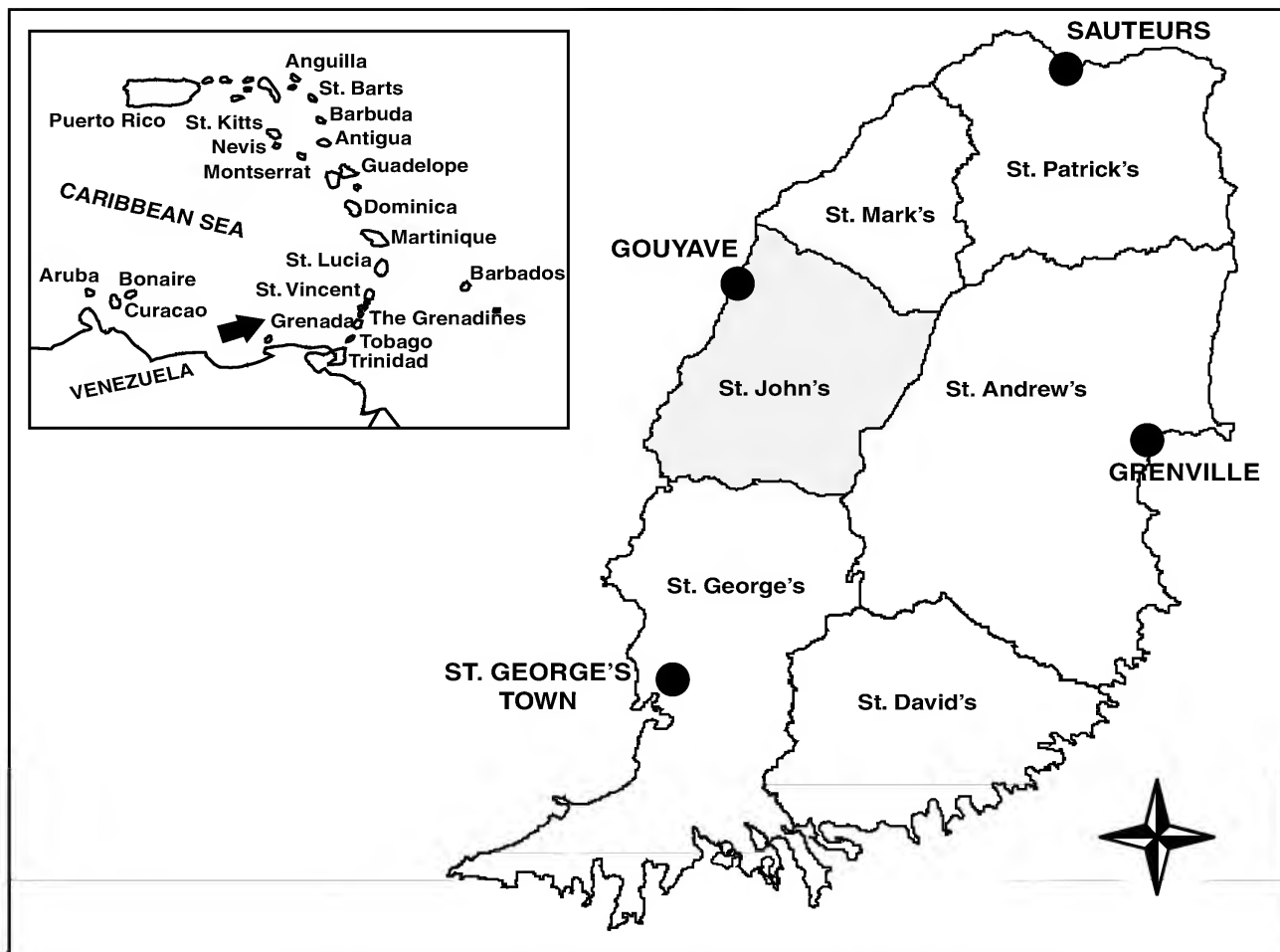


Figure 1. The study area: Grenada and the eastern Caribbean.

living, especially in developing countries (Chambers and Conway 1992, Ellis 2000, Allison and Ellis 2001). Of particular importance is the question of strategies used by households to secure their livelihood. In many poor and rural communities throughout the world, household survival depends upon the ability to develop a diverse array of livelihood activities and strategies (Chambers 1997, Ellis 2000, Ellis and Allison 2004).

Comitas (1962) observed in rural Jamaican communities that no single livelihood activity was lucrative enough for full-time specialization; therefore, households engaged in numerous social and economic activities to secure a living. Livelihood diversification is generally good for poor and rural households because it is an effective strategy for individuals to accumulate assets with which they can construct their own exit routes out of poverty (Ellis and Allison 2004), and it reduces the vulnerability of the poor (Marschke and Berkes 2006).

In fishing communities around the world, a number of livelihood diversification strategies have been documented. They include:

- Occupational pluralism, to widen the income-earning portfolio (Comitas 1962, Panayotou 1986, Rubenstein 1987, Allison and Ellis 2001);
- Flexibility in fishing activities, using different types of gear (Allison and Ellis 2001);
- Geographic mobility, fishing in different areas (Allison and Ellis 2001);
- Specialist-generalist alteration, operating in one fishery or multiple fisheries (Smith and McKelvey 1986);
- Dependency, making claims on relatives, friends, and government (Chambers and Conway 1992); and
- Modification of consumption patterns (Davis 1996, Ellis 1998).

An underlying reason for livelihood diversification is the seasonality of the resource base: "... fishing is a high-risk occupation, and one prone to seasonal and cyclical fluctuation in stock size and location... Diversification reduces the risk of livelihood failure by spreading it across more than one income source. It also helps to overcome the uneven use of assets (principally labor) caused by seasonality" (Allison and Ellis 2001, p. 383). Diversification

reduces vulnerability in the face of widespread market failures and uncertainties, and includes the ability to switch activities as necessary (Chambers 1997).

Through the application of the concept of sustainable livelihood this paper aims to further the understanding of diversification as a strategy by which fishing communities survive. We were interested in the usefulness of livelihood diversification for understanding the social and economic structure of the fishing community, and to use this understanding to inform fisheries management. The analysis highlights how the community of Gouyave whose economic base is pelagic fishing was able to use a diverse array of livelihood strategies to reduce its vulnerability to economic collapse.

The paper begins with an overview of the study area and research methods, and then describes how people make a living in the fishing community of Gouyave. This includes an examination of livelihood activities, diversification strategies, and seasonal patterns of main income sources (fishing, micro-business, and agriculture). The final section explores how livelihood considerations can be included in fisheries management.

STUDY AREA AND METHODS

Study area

Grenada is an island nation in the Eastern Caribbean, situated between latitudes 11°00'N and 12°30'N with a total area of 311 km² (Figure 1). The town of Gouyave, in the parish of St. John's is located on the west coast of the island about 19 km to the north of St. George's town by road. In 2001, Gouyave had an estimated population of 2,152 or about 2% of the nation's population. Of the estimated 2,200 fishers in Grenada, over 300 operate from Gouyave. The town has over 441 residential buildings and 112 commercial, housing 24 different commercial activities. The town has electricity and piped water, a developed network of roads, and access to an international airport to facilitate exports to Caribbean and international markets.

Gouyave has a multi-species and multi-gear fishing industry. The fishery is classified as small-scale, exploiting stocks of small and large pelagics (tuna, mackerel, billfish, flyingfish, dolphinfish, barracuda), coastal pelagic stocks (jack, bigeye scad, rainbow runner), and deep slope and reef demersal stocks (grouper, red hind, snapper). In terms of quantity and fishing effort, the main fish species are yellowfin tuna (*Thunnus albacares*), white marlin (*Tetrapturus albidus*), blue marlin (*Makaira nigricans*), common dolphinfish (*Coryphaena hippurus*), sailfish (*Istiophorus albicans*), swordfish (*Xiphias gladius*), blackfin tuna (*Thunnus atlanticus*), wahoo (*Acanthocybium solandri*), bigeye tuna

(*Thunnus obesus*), and skipjack (*Katsuwonus pelamis*).

The main gear types are surface longline (over 82% of fishers), bottom longline, handline, beach seine, trolling, bankfishing (bottom handline), seche (a jigging handline technique), gillnet, and fish pot. The 3 categories of fishing vessels are the pirogue, launcher, and double-ender. There are 2 types the pirogue—open and cabin. Open pirogues are semi-decked, wooden, between 5–7 m long, powered by a single 15–40 hp outboard engine, and equipped for multiple-purpose fishing. Cabin pirogues, made from wood and/or fibreglass are 7–9 m long, powered by two 40–75 hp outboard engines, and equipped for longline fishing. The second category includes launchers made from wood and fiberglass. These are 9–15 m in length, powered by a 130–300 hp inboard diesel or gas engine, and equipped for overnight longline fishing. The third vessel category is the wooden double-ender powered by oars and equipped for beach seine fishing. A boat census conducted in Gouyave (2003) revealed there were 97 open pirogues (25 inactive), 26 cabin pirogues (6 inactive), 8 launchers, and 6 double-ender boats.

Methods

Data were collected between December 2002 to March 2004 by using secondary data sources, participant observation, semi-structured interviews, and a quantitative survey (Grant 2006). Published documents and reports provided background information on the demographics of the community and number of households. Participant observation involved working alongside selected individuals while they went about their daily activities. Detailed semi-structured interviews were conducted with 20 community members to obtain information as to how they provide food and income for their households, livelihood strategies, social support, and the roles of males and females in the household and community. This information was the basis for a more focused quantitative livelihood survey administered to 169 individuals. This survey focused on the strategies used by individuals involved primarily in fishing as compared to non-fishing livelihoods. Research findings from the quantitative survey were supplemented with semi-structured interviews and other methods to check for consistency in response. Quantitative analysis was performed using SPSS software.

HOW PEOPLE MAKE A LIVING

The following paraphrased quote is a fisher's response to the question: "How are you able to support your family?"

"I am a crew member on a large longline vessel, going to sea 2–4 d at a time. When I am not fishing I work on

TABLE 1

Primary, secondary, tertiary, and other sources of income by gender ($N = 169$).

Occupation Category and group	Principal income source			Secondary income source			Tertiary income source			Other source		
	Male	Female	Total	Male	Female	Total	Male	Female	Total	Male	Female	Total
Fishing livelihood												
Fishing	66	1	67	22	1	23	8	—	8	4	—	4
Fish vendor	7	6	13	7	5	12	1	1	2	—	1	1
Support services	10	—	9	7	—	7	2	—	2	1	—	1
Fish processing worker	3	—	3	1	—	1	—	—	0	—	—	0
Sub-Total	86	7	93	37	6	43	11	1	12	5	1	6
Non-fishing livelihood												
Micro-business	7	7	14	5	17	22	6	1	7	2	—	2
Agriculture												
Nutmeg processing	—	9	9	—	—	0	—	—	0	—	—	0
Gardening	1	1	2	14	—	4	3	—	3	3	—	3
Government worker	7	3	10	3	7	10	4	1	5	1	—	1
Retired	5	4	9	—	—	0	—	—	0	—	—	0
Homemaker	—	8	8	—	1	1	—	—	0	—	—	0
Construction	6	—	6	6	—	6	7	—	7	1	—	1
Service industry	—	4	4	4	1	5	3	—	3	1	—	1
Student	4	—	4	—	—	0	—	—	0	—	—	0
Domestic worker	—	3	3	—	2	2	—	—	0	—	—	0
Professional	1	1	2	—	—	0	1	—	1	—	—	0
Tourism	1	1	2	—	—	0	—	—	0	—	—	0
Sub-Total	32	41	73	32	28	60	24	2	26	8	0	8
No livelihood	—	3	3	—	—	0	—	—	0	—	—	0
Total	118	51	169	69	34	103	35	3	38	13	1	14

my farm, or repair nets, and make sacs and ‘bazor’ [fishing gear] for other fishermen. During fishing off-season, July to September, I use my small wooden boat to go snapper fishing using bottom longline or bankfishing; and during the fishing season I rent this same boat to the beach seine fishery. The income from snapper fishing is very small compared to longlining, but I am able to eat and make some extra money for my family. I have to support my wife and 6 children.

“I rent 3 acres [1.2 ha] of agricultural land, just one mile [1.6 km] from my house. I plant nutmeg (*Myristica fragans*), cocoa, banana, corn, yam, and pigeon peas. Nutmeg is my highest income crop, so I spend a lot of time picking, removing mace, drying, and transporting it to the Nutmeg Pool [Grenada Cooperative Nutmeg Association]. My wife and children help me a lot, especially with drying nutmegs and ‘shelling’ pigeon peas.

“I would say I spend about 90% of my time fishing and 5% on agriculture, but I earn 80% of my income from fish-

ing and 15% from agriculture. These days, it is very difficult to make ends meet. You have to do a number of different things to support your family, and you also have to give a little to your neighbor because you can never tell what will happen to you tomorrow; you may need the help.”

Thus, to take care of his family, this individual was involved in a diverse number of livelihood activities, which was common among fishers and community members.

Diversification strategies in Gouyave

Livelihood diversification. Economic livelihood activities available to community members are summarized in Table 1, while Table 2 lists their specific occupations within the fishing and non-fishing groups. Male and female respondents were involved in 1–7 livelihood activities with most individuals involved in two. Household livelihood strategies ranged from situations where only the head of household engaged in economic activities to those where all household members worked sometimes at more than one activity.

For males, fishing was the principal income source; other important activities were micro-business, agriculture, government, and construction. Females did little or no fishing (only one female fished regularly with her male partner); however, they were involved as vendors and investors. Regarding non-fishing livelihood activities, women were employed in agriculture mainly as nutmeg processors at the GCNA receiving station in Gouyave. The second livelihood activity for women was homemaking or staying home to care for children and elderly relatives, and the third was micro-business.

When consideration is made of the respondents' various sources of income, the importance of fishing is evident (Table 1). Fishing was the sole source of income for 21% of respondents, while the remainder combined fishing and non-fishing activities. Figure 2 shows that by separating principal income sources on the basis of fishing and non-fishing activities, fishing activities are integrated into the scheme of secondary and tertiary income sources. Thus, a man whose main livelihood was construction could participate in beach seine hauling early in the morning prior to work or at weekends.

Fishing diversification. Fishers were involved in multiple fishing activities by combining specialization (a single activity) and multi-tasking (several fishing activities).

Role specialization and multi-tasking. Of the 67 individuals involved in fishing as a principal occupation, 43% combined different roles (Table 3). For example, a boat owner could spend much of his time as captain of his own boat yet might also crew or captain another boat.

Gear specialization and multi-tasking. Of fishers involved in fishing as a principal occupation, 27% were specialists using only longline gear while 66% combined specialization and multi-tasking by specializing in the longline gear but also switched to beach seine, bottom longline, handline, bank fishing, seche, gillnet, fish trap, and vertical longline. About 10% of fishers were no longer involved in longline fishing because of their age; they lacked the physical strength to handle the gear.

Combining fishing occupations. Of the fishers involved in fishing as a principal occupation, 33% mixed fishing occupations (Table 4). Although most fishers were specialists in longline, they performed other fishing occu-

TABLE 2

Occupation grouped under general headings and actual occupation by fishing and non-fishing livelihood activities in Gouyave. ¹'Lambia' or boat helper is an individual who works for a boat owner or captain removing fish from the boat, cleaning the boat, purchasing gas, and making sure the boat was ready for the next fishing trip. ²cleans roadside drains.

Occupation category and group	Occupation
Fishing livelihood	
Fishing	Sailor/crew, captain, boat owner and captain, boat owner
Fish vendor	Retail vendor, retail distributor, wholesale distributor, 'conductor/driver', opportunistic vendor
Support service	Boat builder, boat repair, 'lambia' ¹ or boat helper, engine repair, clean fish
Fish processing worker	Manager, clerk, worker, driver
Non-fishing livelihood	
Agriculture	Farmer, laborer, nutmeg processor
Construction	Masonry, carpenter, bricklayer, contractor, electrician, house painter, plumber, tile layer, welder, road construction
Domestic worker	Cook, washerwoman, servant, babysitter
Government worker	Civil servant, police, fire, postal employee, road worker ² , port worker
Homemaker	Stay home and take care of children, home care for elderly
Micro-business	Entrepreneur, hairdresser, barber, land owner, restaurant/shop owner, dressmaker, shoemaker, street vendors (petty, mobile restaurant and bar)
Professional	Teacher, manager, nurse, accountant, pilot, clerk
Service industry	Bartender, waiter, janitor, sales person, shop keeper, security guard, entertainer
Student	Primary, secondary, vocational
Tourism	Craft maker, craft vendor, hotel worker, bus tour operator

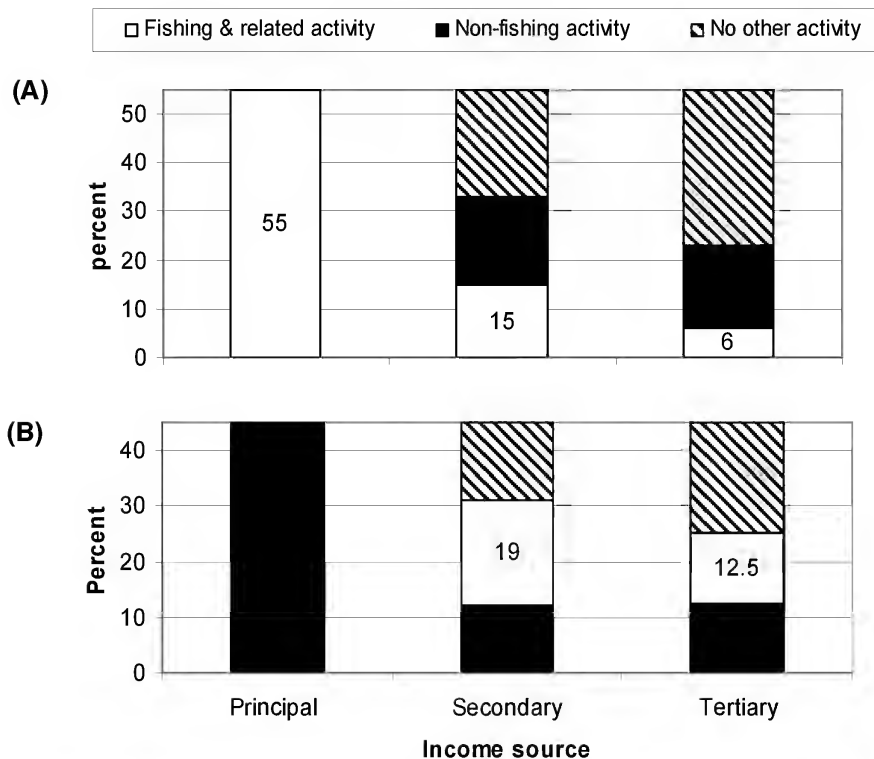


Figure 2. The distribution of respondents involved in fishing livelihood (A) and respondents involved in non-fishing livelihoods (B) their secondary and tertiary income source.

pations, such as selling fish and working part-time as a boat helper. They switched from one fishing occupation to another, with the exception of engine repair and boat building which required special training.

Community's social security net. When household heads were asked if they were able to adequately support their household, 43% said 'yes', 40% said 'barely' (only able to meet immediate financial obligations), 16% said

'no', and 1% gave no response. Although fishers on the whole made a basic living from fishing and related activities by local standards, over half of the respondents were barely able to achieve economic security. It was noted that in the absence of a cash income, households relied on regular assistance in cash and in-kind from family and friends, both locally and overseas (66%), while 25% received no such assistance. Of households reporting they could adequately support themselves, 30% indicated they also received some assistance from families and friends. Such assistance included gifts of fish (43%), gifts of cash (24%), cooking and sharing meals (17%), grooming hair (5%), cleaning fish, domestic assistance, providing loans (4% each), and giving away food crops (3%). Only 2% reported they were unable to give because they needed assistance.

Gifts of fish were common as 93% of fishers reported disposing of a mean of 16 kg of pelagic fish to members of the community after each trip. Often the head and tail sections, and organs of yellowfin tuna destined for export were given away, although left over bait and pieces of sailfish and dolphinfish were also dispensed. These gifts helped sustain households as the fish was either used for home consumption or sold. Those who gave did so in anticipation that if at some future time they were to fall on hard times their generosity would be remembered and

TABLE 3

Role of fishers whose principal income source is fishing ($N = 67$). *Up to 11% of boat owners/investors are involved in fishing as secondary and other income sources.

Role in fishing	Percent
Crew	33
Captain	24
Boat Owner/Captain	21
Boat Owner/Investor*	1
Boat Owner/Investor and Boat Owner/Captain	5
Boat Owner/Captain and Crew	6
Boat Owner/Captain and Captain other owners' boat	6
Captain and Crew	3
Boat Owner and Captain other owners' boat	1
Total	100

TABLE 4

Number of respondents whose principal income source is fishing livelihood and other income source involves fishing and related activities.

Principal fishing livelihood	Other fishing livelihood					Total
	Fishing	Fish vendor	Boat helper	Rent boat	Sell fishing equipment	
Fishing	–	3	1	7	–	11
Fish vendor	2	–	–	–	–	2
Support services						
Boat helper	2	1	–	–	–	3
Engine repair and maintenance	2	–	–	–	–	2
Fish cleaner	–	1	1	–	–	2
Fish processing worker	–	–	–	1	1	2
Total	6	5	2	8	1	22

reciprocated. These traditional customs have reinforced strong social relationships in the community.

Seasonal livelihood patterns

The economic activities of fishing, agriculture, and related spin-off businesses are seasonal and result in household incomes fluctuating over the year. The following discussion reveals the variation for each of these activities.

Fishing. Income from fishing is related to the peak harvesting periods of the principal species (Table 5). The

TABLE 5

Peak harvesting periods for main fish species and gear caught by fishers in Gouyave (shaded). Source: Key interviewees.

Season	Month	Longline gear				Other gears			
		yellowfin tuna	sailfish	marlin	dolphinfish	snapper	blackfin tuna	flyingfish	jack
Dry	Jan								
	Feb								
	Mar								
	Apr								
	May								
	Jun								
Wet	Jul								
	Aug								
	Sep								
	Oct								
	Nov								
	Dec								

highest income-generating species were yellowfin tuna, sailfish, and marlin; medium-income earners were blackfin tuna and dolphinfish; whereas flyingfish, jacks, and snappers were the least valuable. On this basis, the most lucrative period for fishers was from March to August. In terms of the social significance that comes from the giving of fish, then flyingfish and jacks were most important. Since their availability extends from February through until the end of October (Table 5), the generosity of fishers helps sustain the community for the greater part of the year.

Agriculture. Seasonality of farming activities stems from the uneven distribution of annual rainfall. With the first 5 months of the year being dry, the time for land preparation and subsequent planting occurred between May and August, except for some vegetable crops that were irrigated. Throughout the remainder of the year various crops were harvested (Table 6). Those cultivating plants regarded themselves as gardeners as distinct from farmers who were considered to have a greater commitment to land than they did. For most, gardening was a subsistence-type strategy that was done during one's discretionary time on land that was rented or owned.

From discussion with 6 fishers who worked the land, 2 types of gardening were identified: the kitchen garden variety that could be found on any available land associated with the house spot; and a larger garden that existed on plots of land some distance from the house, in one case 11 km away. On the former, crops such as cabbage, corn, dasheen, pigeon peas, and tomatoes might be grown. Usually no more than a few hours per day were spent on weeding and watering these crops that were destined for household consumption. Large gardens, ranged from 0.1–2 ha, had a variety of fruit trees, bananas, traditional export crops (cocoa and nutmeg), roots and tubers, as well as corn and pigeon peas. These gardens were visited 2–4 times a

TABLE 6

Planting (grey) and harvesting (black) of main crops planted by gardeners in Gouyave.

Seasons	Months	root and tubers ¹	corn	pigeon peas	sorrel	vegetables ²	fruits ³	citrus ⁴	bananas ⁵	nutmeg	cocoa
Dry	Jan										
	Feb										
	Mar										
	Apr										
	May										
	Jun										
Wet	Jul										
	Aug										
	Sep										
	Oct										
	Nov										
	Dec										

Source: Key interviewees key:

¹ roots and tubers – dasheen, tannias, yams, potatoes² vegetables – cabbage, carrots, sweet pepper, lettuce, tomatoes³ fruits – golden apples, mangoes, guavas, soursop, plums, sapodillas, cherry⁴ citrus – oranges, grapefruits, tangerines⁵ bananas – bluggoes, bananas, plantains

week, with the entire family providing assistance at key harvesting times. Besides supplying their households with staples, these lands were a source of cash crops that were sold to national outlets such as nutmegs to the GCNA, cocoa to the Grenada Cocoa Association (GCA), and fruits and vegetables to the Grenada National Marketing and Importing Board and local vendors.

Spin-off businesses. Since these activities involved the processing of fish and agricultural commodities they have corresponding seasonal cycles (Table 7). For example, when flyingfish were in season women perform the value-added work of filleting, packing, and selling them. Similarly when jacks were abundant women continue the long-standing tradition of cleaning and sun-drying them prior to selling them in Grenville, a town off Grenada's east coast (Figure 1). Farm commodities, during their respective harvesting season, were prepared in a number of ways. For instance, fruits were washed, bagged, and sold either on the street or in markets. Corn cobs were roasted in roadside coal stoves for sale. Pigeon peas were shelled, sorted, and bagged for sale. Cocoa beans not sold to the GCA were made into cocoa balls by grinding the beans, adding spices, and rolling into balls for later use

in making hot beverage. Sorrel (fleshy sepal of a tropical plant Roselle) was stripped, bagged, and sold to make a drink. A few enterprising individuals set up mobile bars ('igloo' containers on wheels) from which they sold alcohol and drinks and mobile restaurants (portable stove on a table) from which they sold fried chicken, fish, and fries. Activities such as these are practical cottage industries that augment household incomes.

MANAGING THE "HUMAN SYSTEM" IN FISHERIES

The importance of fishing to the community

The idea of sustainable livelihood in Gouyave involves maintaining a diverse portfolio of livelihood activities and strategies, as elsewhere in rural communities in the Caribbean. Such strategies include livelihood diversification that involves combining incomes from fishing, agriculture, construction, and micro-businesses; and fishing diversification where fishers switch to alternative gear, roles, and occupations to take advantage of species availability and fishing livelihood activities.

Fishing is the main economic contributor to the local economy, as it provides food, income, direct and indi-

TABLE 7

Monthly peak harvesting of fish and agricultural commodities and the resulting spin-off business activities.
YFT= yellow fin tuna; BFT = black fin tuna.

Month	Fish commodities	Agricultural commodities	Spin-off micro-business activities
JAN	sailfish		pigeon peas
FEB	sailfish, flyingfish, marlin	reap yams, pigeon peas, cash	
MAR	YFT, BFT, flyingfish	crops, bananas, cocoa	
APR	YFT, BFT, flyingfish		fillet flyingfish, 'cocoa balls'
MAY	YFT, BFT, flyingfish, marlin		
JUN	YFT, BFT, jack, marlin	planting season	mobile restaurants
JUL	YFT, BFT, jack		dried jack
AUG	YFT, BFT, jack		mobile restaurants, roast corn, fruits
SEP	BFT, jack, snapper		Roast corn, fruits, dried jack
OCT	BFT, jack, snapper	reap yams, corn, pigeon peas,	roast corn, dried jack
NOV	sailfish	sorrel, cash crops, fruits, cit-	
DEC	sailfish	rus, nutmeg	pigeon peas, sorrel

rect employment, and micro-business opportunities. It has evolved into the main contributor because of poor employment opportunities in Grenada. Fishing is also an accessible occupation as no fishing license or formal training is required, as training is done on the job with a competent captain. Likewise, to purchase fishing equipment, fishers can apply for a loan at the bank or through the Fisheries Division. Fishers also have access to international markets via government and private sector organizations to export fish.

Expenditures for and earnings from fishing are channeled back to the community, creating an economic multiplier effect. The economic multiplier is manifested by income from fishing consumed in the community on food, alcohol, clothing, and entertainment. When fish catches are high, income and consumption increase, this creates jobs for other community members in the service sector. It is possible to tell by walking down the street in Gouyave if fishers are catching fish. If the streets are relatively quiet with a number of shops closed, one can tell that no fish has been caught lately. However, if people are in the streets, the bars are open late, and there is merriment then the fishery is doing well.

Fishing helps to build social relations and cultural identity (Jentoft 2000). Social relations in the community, built on reciprocal obligations, revolve around fish. The sharing and exchanging of fish for cash (non-commercial transaction) and in-kind assistance help to maintain connections with family and friends in the community, in other communities, and abroad. Social relations and cultural rules regarding the sharing of fish provide a social safety net to help support households that are in need.

The diversity and complexity of livelihood spreads the flow of income and food across the seasons, making households more stable and less vulnerable to the uncertainty in food production and of daily life (Chambers et al. 1981, Sahn 1989). The seasonality of fish and agricultural commodities works for the benefit of households by allowing community members to switch between and among fishing and non-fishing livelihoods. Such fluidity is the key to a successful livelihood strategy.

Management implications

To include social objectives in fisheries planning and management, a key implication of the findings is that management options based solely on fisheries science, such as effort reduction, quotas, and other conservation measures, should not be instituted without first considering their social and economic implications. Fishing is the social and economic thread that binds fishers and community members together as fish are eaten, bartered, exchanged for cash and services, used to repay debt, and meet social obligations. Therefore, any major crisis or change in policy could cause widespread repercussions in the community and the island state.

Conventional management tends to take a single-species approach. What is needed instead is an ecosystem based management approach that takes into consideration the complex multi-species, multi-gear nature of the fishing industry where fishers are continuously altering their fishing practice, gear, and fishing area to exploit multiple resources in the seasonal round. The management of large pelagic species needs to consider coastal pelagic species that are used as bait in the pelagic fishery. Likewise,

conservation measures for one fish species could increase the exploitation of another. Ecosystem based management gives fishers the flexibility to switch between different species according to season and boosts spin-off micro-businesses which increases households stability.

Fishing as part of a broader livelihood context needs to be managed with attention to both fishing and non-fishing livelihoods. The problem is that non-fishing sectors are outside the mandate of Fisheries Division, and government agencies do not collaborate well with each other; promoting sustainable livelihoods for communities will require such horizontal collaboration. As well, regional/international fisheries regulations can impact livelihood. Hence, improved communication through the establishment of linkages, across the various levels of management from the community to regional and international levels (i.e., vertical linkages), is important for community livelihood (Grant 2006, Berkes 2006).

In conclusion, to manage fisheries with attention to social and economic as well as biological objectives, managers need to understand the livelihood systems of fishing communities (Pomeroy and Rivera-Guieb 2006, Allison and Ellis 2001). Such livelihood systems involve fishing diversification, including seasonal changes in species and gear, and taking a multi-species approach. They also involve livelihood diversification at the local level with attention to sectors such as micro-business, agriculture, tourism, and construction. Integrating social objectives into fisheries management would involve a number of conditions that do not exist in the present fishery: building horizontal linkages between the Fisheries Division and other agencies, and vertical linkages between fishing communities and the various levels of management (national and international), through increased collaboration, communication, and understanding.

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Alexia Morgan

Florida Museum of Natural History

George H. Burgess

Florida Museum of Natural History

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AT-VESSEL FISHING MORTALITY FOR SIX SPECIES OF SHARKS CAUGHT IN THE NORTHWEST ATLANTIC AND GULF OF MEXICO

Alexia Morgan* and George H. Burgess

Florida Program for Shark Research, Florida Museum of Natural History, Dickinson Hall,
University of Florida, Museum Road, Gainesville, FL 32611 USA, *E-mail amorgan@flmnh.
ufl.edu

ABSTRACT From 1994–2005 the Commercial Shark Fishery Observer Program (CSFOP) placed fishery observers aboard US bottom longline vessels engaged in directed fishing for sharks in the region from New Jersey to Louisiana, USA. Observers routinely recorded species specific at-vessel mortality as related to enduring the stress of longline capture. Data for 5 species of sharks (sandbar *Carcharhinus plumbeus*, blacktip *Carcharhinus limbatus*, dusky *Carcharhinus obscurus*, tiger *Galeocerdo cuvier*, scalloped hammerhead *Sphyrna lewini*, and great hammerhead *Sphyrna mokarran*) were analyzed in this study. Multiple stepwise linear regressions indicate that age group, soak time and bottom water temperature can be used as predictors of at-vessel mortality and that size restrictions, size selective gear, restricting the soak time and time/area closures may be beneficial to fisheries targeting large coastal sharks.

RESUMEN El Programa de Observación de la Pesquería Comercial de Tiburones sitió observadores durante el periodo 1994–2005 en naves pesqueras dedicadas específicamente a la pesca con palangre de especies costeras grandes de tiburones en la región comprendida entre los estados de New Jersey y Louisiana en la costa estadounidense. Estos observadores tomaron datos sobre la habilidad de diferentes especies para sobrevivir el estrés de la captura con palangre. En este estudio analizamos datos de seis especies (*Carcharhinus plumbeus* o tiburón trozo, *Carcharhinus limbatus* o tiburón macuira, *Carcharhinus obscurus* o tiburón arenoso, *Galeocerdo cuvier* o tintorera tigre, *Sphyrna lewini* o cornuda común, y *Sphyrna mokarran* o cornuda gigante). El múltiplo el retroceso lineal progresivo indican que el uso de restricciones por tamaño, tiempo en el agua, tipo de equipo y el cierre de pesquerías por área o por periodo pueden beneficiar el manejo de las pesquerías de tiburones costeros grandes.

INTRODUCTION

Management of sharks in the western north Atlantic Ocean and Gulf of Mexico (GOM) waters of the United States has been politically, socially, economically and biologically contentious. For more than a decade, resource managers, fishery biologists and fishers have struggled to create a management plan that would allow sustainable fishing and economic viability for fishers. The exploitation of shark resources in this region has greatly increased over the past 2+ decades (NMFS 1994, 1998, 2006). Stock assessment results have varied for individual species but generally conclude that shark mortality as a result of fishing (commercial and recreational) has exceeded the reproductive capacity of certain species to the detriment of overall stock size.

Sharks are susceptible to overfishing because of their K-selected life history characteristics (Heppell et al. 1999, Cortés 1999, 2002). Many species important to commercial and recreational fisheries grow slowly, have later ages of maturation, and a limited reproductive capacity. It has been estimated that several of the more important shark species in the fishery such as the sandbar (*Carcharhinus plumbeus*) (Sminkey 1994, Cortés 1999) and dusky (*Carcharhinus obscurus*) (Simpfendorfer 1999) sharks have a capacity to increase their population size at <10% per year. Musick et

al. (2000) noted that species with intrinsic rates of increase <10% were particularly vulnerable to excessive mortalities and rapid population declines.

In addition, several species of shark commonly caught in the bottom longline shark fishery, including the dusky, great (*Sphyrna mokarran*) and scalloped hammerheads (*Sphyrna lewini*), suffer from very high at-vessel fishing mortality rates (Morgan and Burgess unpublished data, University of Florida, Gainesville, FL). At-vessel fishing mortality pertains to whether individual sharks are alive or dead when brought on board the vessel (i.e., death results directly from the in-water fishing process). An individual shark species' at-vessel fishing mortality rate has a large impact on the success or failure of management plans designed to protect it. Management techniques such as quotas and prohibited species are based on the assumption that individuals of regulated species are returned to the sea alive. This assumption is erroneous if the regulated species has high at-vessel fishing mortality.

Although sharks historically have been managed as groups (large coastal, small coastal, pelagic, prohibited and dogfish; NMFS 1999), future management of sharks in the northwest Atlantic and GOM will likely be species specific. Therefore, we analyzed our at-vessel mortality data set for information on species specific viability as related to enduring the stress of longline capture. Sandbar, black-

tip (*Carcharhinus limbatus*), dusky, tiger (*Galeocerdo cuvier*), scalloped hammerhead, and great hammerhead sharks were analyzed to determine if there was a difference in at-vessel mortality rates between species, gender, age groups, longline fishing soak times and bottom water temperature. These species represent one prohibited species (dusky), the 4 most commonly caught large coastal species in the fishery, and the great hammerhead (large coastal). This latter species is of particular interest due to its high at-vessel mortality and that it mirrors that of the abundant scalloped hammerhead (Morgan and Burgess unpublished data, University of Florida, Gainesville, FL).

METHODS

The Commercial Shark Fishery Observer Program (CSFOP) placed trained fishery observers aboard commercial bottom longline vessels targeting sharks from New Jersey to Louisiana from January 1994 to April 2005. Fishing vessels primarily deployed heavy-duty monofilament mainlines ranging in length from 1.9–44.5 km, with 53–2,835 hooks attached to the ends of 1.8–2.4 m gangions. Hooks ranged in size from 3/0 to 20/0 and primarily consisted of circle hooks, although some “J” hooks were employed. The mainline was anchored to the bottom using weights during the setting of the gear and gangions were set at or near the bottom. Gear typically was set at sunset and hauled back the following morning near dawn.

Fishery observers were trained in species identification and data collection prior to deployment. Observers collected catch and effort data from each longline set targeting sharks. Fishing gear configuration used during individual bottom longline sets was documented prior to the start of each set. The times when the first and last hooks entered and were removed from the water were recorded by the observer during the setting and retrieval of the gear. Soak time (hr) is defined as the interval between the time the first hook entered the water until the first hook was removed from the water. The bottom water temperature (°C) was recorded by a Stowaway XTI temperature/depth recorder (Onset Computer Corporation) attached to the mainline during the set and subsequently downloaded onto a laboratory computer. Individual caught sharks were brought on board the vessel and identified to species, measured (cm FL), sexed and condition noted as alive/dead. Data was archived at the Florida Museum of Natural History were prior to analysis.

Data from 8,583 sandbar, 1,982 blacktip, 2,466 tiger, 662 dusky, 455 scalloped hammerhead, and 178 great hammerhead sharks were analyzed in this study. This subset was utilized because there was not corresponding data

on the soak time and/or bottom water temperature on all sets made during the study period. Data was analyzed by gender (female and male) and 3 FLs derived age groups (age-0, juvenile and adult). The sandbar was considered age-0 at FLs from 0–60 cm, juvenile from 61–150 cm and adult at >150 cm (Mearson and Pratt 2001). Blacktips were considered age-0 at FLs from 0–75 cm, juvenile from 75–115 cm and adult at >115 cm (Carlson et al. 2006). Tigers were considered age-0 at FLs from 0–06 cm, juvenile from 107–257 cm and adult at >258 cm (Natanson et al. 1999). Dusky were considered age-0 at FLs from 0–100 cm, juvenile from 101–231 cm and adult at >231 cm (Natanson et al. 1994). Scalloped hammerheads were considered age-0 at FLs from 0–65 cm, juvenile from 66–137 cm and adult at >137 cm (Branstetter 1987). Great hammerheads were considered age-0 at FLs from 0–80 cm, juvenile from 101–189 cm and adult at >190 cm (Castro 1983, Stevens and Lyle 1989). Soak times were broken into six 4-hr bins (0–4 hr, 5–8 hr, 9–12 hr, 13–16 hr, 17–20 hr and >20 hr) and bottom water temperature was broken into six 5° bins (0–10° C, 11–15° C, 16–20° C, 21–25° C, 26–30° C and >30° C). Mortality for each species was calculated by dividing the total number of dead sharks caught by the total number of sharks caught by gender, soak time, age group and bottom water temperature category.

We performed a multiple stepwise linear regression for each individual species, using mortality as the dependent variable and gender, soak time, age group and bottom water temperature as independent variables. Variables had to be significant at $P < 0.15$ before they could be entered into the model and had to be significant at $P < 0.10$ to remain in the model (Murphy et al. 1995). Species (1–6) and gender (1=female and 0=male) were coded with dummy variables. Median values were used for soak time bins, bottom water temperature bins and age groups. The proportion of dead animals (for each gender, age group, soak time bin and bottom water temperature bin) by species were arcsine transformed (prior to regression analysis) to meet the assumption of normality (Diaz and Serafy 2005). All other assumptions of multiple linear regressions (linearity, X is measured without error, homoscedasticity, independent variables and random sampling) were met. All analyses were performed using SAS 9.1 (SAS Institute, Cary, NC).

RESULT

Sharks ranged in FLs from 54–214 cm for the sandbar, 59–165 cm for the blacktip, 53–318 cm for the tiger, 61–289 cm for the dusky, 56–287 cm for the scalloped hammerhead, and 78–330 cm for the great hammerhead

sharks. The tiger shark had the lowest overall at-vessel mortality rate (8.5% total, 9.1% young, 7.6% juvenile, and 37.5% adult), followed by the sandbar (36.1% total, 89.1% young, 41.8% juvenile, and 22.4% adult), dusky (81.1% total, 87.7% young, 82.4% juvenile, and 44.4% adult), blacktip (88% total, 86.4% young, 90.5% juvenile and 87.3% adult), scalloped hammerhead (91.4% total, 70% young, 95.2% juvenile and 90.9% adult) and great hammerhead (93.8% total, 86.4% young, 90.5% juvenile and 87.3% adult) (Table 1).

The regression model including soak time, bottom water temperature and age group explained 46% (adjusted R^2) of the variation in mortality for the blacktip shark ($F=9.9$, $P<0.0001$) (Table 2). Soak time and bottom water temperature had a positive effect on mortality indicating that increases in soak time and bottom water temperature (by one unit effort) would increase mortality while size had a negative effect on mortality indicating that increases in size (by one unit effort) would decrease mortality, when all other variables are held constant (Table 2).

Soak time and bottom water temperature were included in the final model for the tiger ($F=6.7$, $P=0.003$), dusky ($F=6.5$, $P=0.007$) and great hammerhead ($F=10.8$, $P=0.0003$) sharks (Table 2). These models explain 23%, 32% and 39% of the variation in mortality respectively (Table 2). Soak time had a positive effect on mortality for all 3 species and bottom water temperature had a positive effect on mortality for the dusky shark but a negative effect on mortality for the tiger and great hammerhead sharks (Table 2).

The sandbar shark's final model included the variables soak time and age group ($F=19.2$, $P=0.0001$) and explained 44% of the variation in mortality (Table 2). Soak time had a positive effect and size had a negative effect on mortality (Table 2).

The final model for the scalloped hammerhead included the variable soak time ($F=9.1$, $P=0.006$) and explained 24% of the variation in mortality rates for this species. Soak time had a positive effect on mortality (Table 2).

DISCUSSION

Gender does not factor into at-vessel mortality rates but age group, soak time, and bottom water temperature are important predictors of mortality. Studies have shown that size, soak time (Diaz and Serafy 2005) and water temperature (Manire et al. 2001) could affect mortality rates and earlier interim analyses of our data (Burgess and Morgan 2005) have provided evidence of species-specific at-vessel mortality rates. Existing management of sharks in Atlantic waters of the United States has failed

to adequately protect certain species (Cortés et al. 2002, NMFS 2006b) and future management will likely require alternative management tools, such as time/area closures, size limits, and gear modifications (i.e., size-selective gear and reducing the soak time of the fishing gear). The results from this study will give fisheries managers better insight into which factors affect at-vessel mortality for commercially important shark species and which alternative management plans may be most effective.

Size has been shown to be an important component of mortality in various species (Davis 2002). Diaz and Serafy (2005) showed the proportion of blue sharks (*Prionace glauca*) caught on longline gear and returned to sea alive increased with size. Mortality of longline-caught Atlantic cod (*Gadus morhua*) was highest at small sizes (Milliken et al. 1999) and small haddock (*Melanogrammus aeglefinus*) and whiting (*Merlangius merlangus*) caught in trawls had the highest discard mortality rates (Sangster et al. 1996). Our data similarly reveal that at-vessel mortality rates decrease as size increases for sandbar and blacktip sharks. In contrast, great hammerhead and scalloped hammerhead sharks suffered very high at-vessel mortality in all age groups.

The increased physiological stresses caused by capture makes it more difficult for smaller animals to survive the fishing process (Davis 2002). Demographic analysis has shown that changes in juvenile sharks' survival (Heppell et al. 1999, Cortés 2002) has the greatest effect on overall population growth rates. Fisheries managers could use size limits to protect certain age groups from at-vessel mortality rates. Sandbar sharks likely can benefit from size restrictions aimed at protecting the juvenile and young age groups. However, species which suffer from high at-vessel mortality rates in all size classes (great hammerhead, scalloped hammerhead) would not benefit from size limits.

Soak time is an important factor because many carcharhinid and sphyrnid sharks are considered obligate ram ventilators (Carlson et al. 2004), relying on constant movement to force oxygenated water over their gills. The great and scalloped hammerheads (Carlson et al. 2004), blacktip (Manier et al. 2001) and likely the dusky shark are active epibenthic species that are considered obligate ram ventilators, making them more likely to be affected by longer soak times than slower swimming ground sharks. Sharks that rely on ram ventilation must increase either swimming speed and/or mouth gape in order to compensate for decreases in oxygen availability (Carlson and Parsons 2001). It would be very difficult for these species to increase their swimming speed while hooked on a longline, resulting in relatively rapid asphyxiation following hooking. The sandbar shark, a species closely

TABLE 1

The total number of each species caught by age group, the number dead by species and age group, the percent dead by species and age group, and the total number caught, total number dead and percent dead for all species by age group.

Species	Young (total #)	Young (# dead)	Young (% dead)	Juvenile (total #)	Juvenile (# dead)	Juvenile (% dead)	Adult (total #)	Adult (# dead)	Adult (% dead)	Total #	Total dead	Total %
Tiger (<i>Galeocerdo cuvier</i>)	1,289	117	9.1	1,169	89	7.6	8	3	37.5	2,466	209	8.5
Scalloped hammerhead (<i>Sphyrna lewini</i>)	10	7	70.0	105	100	95.2	340	309	90.9	455	416	91.4
Blacktip (<i>Carcharhinus limbatus</i>)	22	19	86.4	419	379	90.5	1,541	1,346	87.3	1,982	1,744	88.0
Great hammerhead (<i>Sphyrna mokarran</i>)	1	1	100.0	71	66	93.0	106	100	94.3	178	167	93.8
Dusky (<i>Carcharhinus obscurus</i>)	293	257	87.7	306	252	82.4	63	28	44.4	662	537	81.1
Sandbar (<i>Carcharhinus plumbeus</i>)	46	41	89.1	5,904	2,467	41.8	2,633	589	22.4	8,583	3,097	36.1
Total	1,661	442	26.6	7,974	3,353	42.0	4,691	2,375	50.6	1,4326	6,170	43.1

TABLE 2

Summary results for multiple stepwise linear regressions for each species, including adjusted R^2 , final variables, degrees of freedom (DF), parameter estimates, standard error ($s_{\hat{\beta}}$), t value and P value.

Tiger (<i>Galeocerdo Cuvier</i>) ($F=6.7$, $P=0.003$)						
$R^2=0.23$	Variable	DF	Parameter estimate	$s_{\hat{\beta}}$	t value	P value
	Intercept	1	0.51	0.23	2.3	0.030
	Soak time	1	0.02	0.01	1.9	0.072
	Bottom water temperature	1	-0.02	0.01	-3.0	0.006
Scalloped hammerhead (<i>Sphyrna lewini</i>) ($F = 9.1$, $P = 0.006$)						
$R^2=0.24$	Intercept	1	1.01	0.16	6.4	<0.0001
	Soak time	1	0.03	0.01	3.0	0.006
Blacktip (<i>Carcharhinus limbatus</i>) ($F = 9.9$, $P < 0.0001$)						
$R^2=0.46$	Intercept	1	-0.02	0.41	-0.6	0.950
	Soak time	1	0.06	0.01	4.8	<0.0001
	Bottom water temperature	1	0.04	0.01	2.9	0.007
	Age group	1	-0.17	0.08	-2.0	0.055
Dusky (<i>Carcharhinus obscurus</i>) ($F = 6.5$, $P = 0.007$)						
$R^2=0.32$	Intercept	1	-0.40	0.50	-0.8	0.400
	Soak time	1	0.04	0.02	2.0	0.060
	Bottom water temperature	1	0.06	0.02	2.0	0.006
Great hammerhead (<i>Sphyrna mokarran</i>) ($F = 10.8$, $P = 0.0003$)						
$R^2=0.39$	Intercept	1	0.62	0.40	1.6	0.120
	Soak time	1	0.07	0.02	4.0	0.0004
	Bottom water temperature	1	-0.03	0.02	-2.1	0.050
Sandbar (<i>Carcharhinus plumbeus</i>) ($F = 19.2$, $P < 0.0001$)						
$R^2=0.44$	Intercept	1	0.60	0.21	2.8	0.008
	Soak time	1	0.04	0.01	5.0	<0.0001
	Age group	1	-0.24	0.07	-3.0	0.002

associated with substrate (Compagno 1984), is also an obligate ram ventilator (Dowd et al. 2006) but does not suffer from a very high at-vessel mortality rate. The sandbar's association with oxygen-poor epibenthic waters and slower ambient swimming speed (inferred from its stocky body), apparently make this species better suited to survival when swimming is confined after being hooked on a longline. The tiger shark, another slow swimmer that makes frequent forays into benthic waters (Compagno 1984), is most likely able to compensate while hooked on a longline, by increasing its mouth gape and using a buccal pump system to force water over its larger mouth.

Fisheries managers may consider putting restrictions on the length of soak time in order to better protect species which rely on obligate ram ventilation and suffer from

very high at-vessel mortality rates. That said, soak time only reveals how long the total gear was in the water but gives no indication of how long individual sharks were hooked on the individual gangions. Our ongoing studies employing hook timers (Boggs 1992) should provide useful information to more accurately characterize the importance of soak time.

Increases in water temperature have been shown to have a negative effect on sharks' survival (Manire et al. 2001) and can lead to acidosis (Heisler 1998). Atlantic salmon (*Salmo salar*) have been shown to suffer higher post release mortality when caught in water $>20^{\circ}\text{C}$ (Wilkie et al. 1996). The warmer water temperature combined with increased activity while hooked, lead to the salmon's inability to fully recover. Species of shark with

the physiological abilities to endure levels of hypoxia and acidosis will fare the best in water temperatures outside their natural range (Carlson et al. 2003). It is possible that individual shark species' behavior when hooked will also affect their ability to survive in different bottom water temperatures. Species that fight while hooked will use more oxygen, which could lead to increased physiological stress and possible death. Fisheries managers could restrict fishing to certain times of year through the use of time/area closures to offset the effects of water temperature on at-vessel mortality.

Future studies should determine how long the sharks are hooked on the longline, ascertain if the length of the gangion has any affect on at-vessel mortality, determine whether the type of hook (i.e., circle or "J") or size of hook affects at-vessel mortality, establish relationships between water temperature, physiological stress and at-vessel mortality for individual species and determine if the behavior of the sharks when hooked affects mortality. Our study gives an understanding of some aspects of bottom longline fishing, which affect at-vessel mortality, but there are still a number of factors that should be looked at in order to provide a full understanding of this type of mortality.

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Erick Castro

San Andres Island, Colombia

Heins Bent

San Andres Island, Colombia

Carlos Ballesteros

San Andres Island, Colombia

Martha Prada

San Andres Island, Colombia

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LARGE PELAGICS IN THE SOUTHERN SECTION OF THE SEAFLOWER MARINE PROTECTED AREA, SAN ANDRES ARCHIPELAGO, COLOMBIA: A FISHERY IN EXPANSION

Erick Castro, Heins Bent, Carlos Ballesteros, and Martha Prada¹

Secretaría de Agricultura y Pesca, Av. Newball, Edificio Coral Palace, 2do piso, San Andrés Island, Colombia. E-mail pescastro@gmail.com

¹Blue Dream Ltd, Perry Hill, San Andres Island, Colombia

ABSTRACT Isolated and sparse reef atolls comprising the southern section of the Seaflower MPA have been traditionally exploited by artisanal fishers using handlines. These practices have severely depleted the demersal fish stock and now fishers have shifted their efforts to the pelagic stock. The pelagic fishery included the extraction of more than 25 species, with *Thunnus atlanticus*, *Acanthocybium solandri*, *Coryphaena hippurus*, and *Katsuwonus pelamis* being the most common. Three years of fishery-dependent data (2004–2006) were used to describe traditional fishing methods and techniques, and to document, for the first time, a declining trend in the large pelagic stock. Pelagic landings accounts for more than 70% of the total landings, and are extracting important fraction of the juveniles depending on the species. Significant changes in CPUE were associated with greater distance from port, although not in the expected order. The status of the large pelagic fish stocks in the archipelago is still unknown, but the results presented in this paper provide baseline information needed to determine the effectiveness of the recently established Seaflower MPA. They also illustrated how primitive gear can still produce a severe reduction in abundances of several stocks, particularly when exploiting remote, small, isolated atolls prone to a serial depletion phenomenon.

RESUMEN Los aislados y dispersos atolones arrecifales de la sección sur del AMP Seaflower han sido tradicionalmente explotados por pescadores artesanales utilizando líneas de mano. Estas prácticas han disminuido significativamente el stock de peces demersales y ahora los pescadores han reorientado estos esfuerzos hacia el stock pelágico. La pesquería pelágica incluye la extracción de más de 25 especies, con *Thunnus atlanticus*, *Acanthocybium solandri*, *Coryphaena hippurus* y *Katsuwonus pelamis* siendo las especies más comunes. Tres años de datos dependientes de la pesquería (2004–2006) fueron usados para describir los métodos y técnicas de pesca, y para documentar, por primera vez, una tendencia decreciente del stock de grandes pelágicos. Los desembarcos pelágicos contribuyen con más del 70% del total de las capturas, y dependiendo de la especie se extrae una fracción importante de juveniles. Cambios significativos en CPUE fueron asociados con mayores distancias desde el puerto, aunque no en el orden esperado. El estatus de los stocks de peces de grandes pelágicos en el archipiélago es aún desconocido, pero los resultados presentados en este trabajo proveen información de línea base necesaria para determinar la efectividad del AMP Seaflower recientemente establecida. También se ilustra cómo artes de pesca simples pueden producir una reducción severa en las abundancias de varios stocks, particularmente cuando se explotan en atolones remotos, pequeños y aislados propensos a un fenómeno de agotamiento en serie.

INTRODUCTION

Located in the western Atlantic, the archipelago of San Andres, Providence and Santa Catalina extends over 250,000 km² of oceanic waters and scattered atolls covered by well developed coral reefs (Diaz et al. 2000). People in the islands and from neighboring countries work for Colombian companies that have been fishing these reefs at artisanal and industrial levels, extracting mainly spiny lobster (*Panulirus argus*), queen conch (*Strombus gigas*) and several species of reef fish (*Lutjanus vivannus*, *Etelis oculatus*, *Mycteroperca venenosa*, *M. bonaci*, among others). As a consequence, declining trends in the reef associated fisheries have been experiencing all levels of extraction (Caldas and Santos 2004, Prada and Castro 2004).

With diminishing demersal stocks, fishing for pelagic fishes has significantly increased, especially in the south-

ern atolls which have narrow insular shelves and are constantly exploited by artisanal fishers (Diaz et al. 1995). Unfortunately, the lack of fishing regulations on any fish stocks has resulted in limited statistics and reduced the capability to scientifically demonstrate any real growth of this fishery, despite the continued use of primitive fishing equipment and gear.

Shifting from a reef dominated fishery to a pelagic dominated fishery should have happened prior to 1995 when pelagic landings accounted for about 50–60% of total landings in the southern atolls (Pomare 1999). Slight increases in pelagic landings (70%) were later reported by Grandas and Castro (2004) and Castro (2005). However, 3 decades ago, artisanal fishers maintained a dominant presence of reef fishes in these areas (Barriga et al. 1969).

Pelagic stocks in the islands included a group characterized for their large size, highly migratory movements

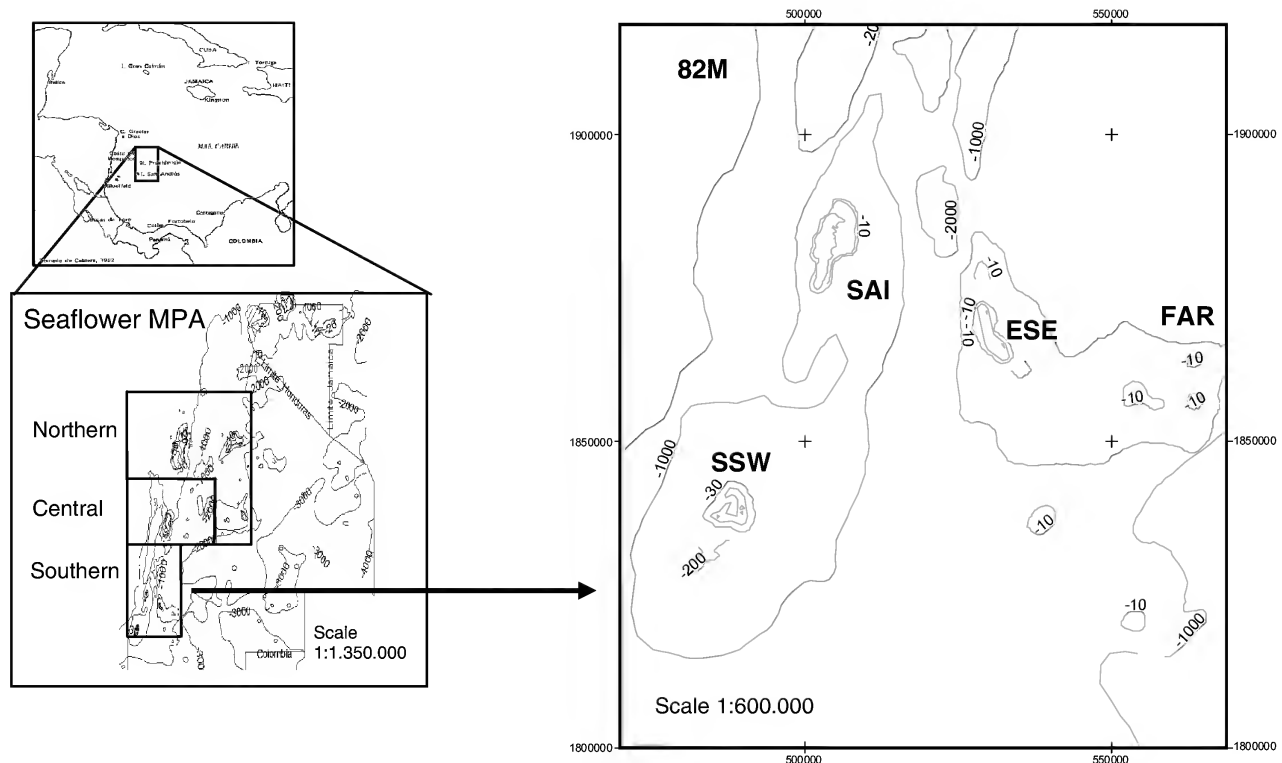


Figure 1. Spatial location of the fishing areas at the southern Seaflower MPA. SAI stands for San Andres Island, ESE for East-South-East reef, SSW for South-South-West reef, FAR for Far Bank and 82M for areas of the 82 Meridian under Colombia jurisdiction.

and trans-boundary distribution. In the islands, they are represented by *Thunnus atlanticus* (blackfin tuna), *T. obesus* (bigeye tuna), *Acanthocybium solandri* (wahoo), *Coryphaena hippurus* (dolphinfish) and *Katsuwonus pelamis* (skipjack tuna), among other species. In addition, there is a second group comprised of those pelagic species living near reefs in coastal waters with a reduced territory (distribution is largely confined to the Western Caribbean) which locally includes *Elagatis bipinnulata* (rainbow runner), *Canthidermis sufflamen* (ocean triggerfish), *Seriola fasciata* (lesser amberjack), *Caranx ruber* (bar jack) and *Caranx latus* (horse-eye jack), among others.

The reduction in fisheries production and the improvement in biodiversity conservation policies have contributed to the implementation of a new economical development model based on the sustainable use of the marine resources. UNESCO declared the archipelago as the Seaflower Biosphere Reserve (BR) in November 2000. Three large sections (65,000 km²) within the BR were designated the Seaflower multiple use Marine Protected Area (MPA) by the Ministry of Environment and CORALINA (the environmental authority in the islands) in June 2005. The existence of closed areas and more efficient fishery management regulations are expected to facilitate a change in the fisheries declines currently experienced, but poorly documented.

This paper analyzed 3 years of fishery-dependent data (2004–2006) on large pelagics from the southern Seaflower MPA region to document fishing techniques and gear, changes in fish landings, species composition and their spatial and temporal patterns from the perspective of the artisanal fishery. It is hypothesized that a) large pelagic CPUE (Catch Per Unit Effort) will decrease with increasing distance from home ports, and b) 50% of the large pelagic landings of the 4 most common species are juveniles. Results from this study can be used by MPA managers to determine baseline information for future assessment of MPA effectiveness on the large pelagics and provide insight towards the debate of a large MPA in the Caribbean could benefit large pelagics.

MATERIALS AND METHODS

Study Area

The Colombian Archipelago, comprised by 3 small inhabited islands (San Andres, Providencia and Santa Catalina) and 7 uninhabited cays and coral banks, is located between 11°30'N to 16°30'N and 78°28'W to 82°W (Figure 1). The archipelago includes a total insular shelf area of 57 km² and an open water marine area of about 250,000 km² surrounded by a deep oceanic environment (maximum

5,000 m). Atolls are aligned in a north-northeasterly direction (Geister 1997), vary in shape and extension, and can be hundreds of nautical miles apart. Each atoll has distinct habitats and productivity rates, thus conferring them with unique ecological characteristics, despite their geologic similarity. In general, reef complexes in the archipelago are characterized by the presence of barrier reefs with shallow and/or deep fore-reefs on the windward side, a central reef lagoon with coral reef patches and slopes of varying grades on the leeward side.

The study area is confined to the southern section of the Seaflower MPA comprised by 3 reef atolls: San Andres (SAI), East-South-East (ESE) and South-South-West (SSW), as well as 2 non-emergent reef banks (FAR and 82M). The 82M is situated on the section of the Nicaraguan rise that belongs to Colombia. According to IGAC (1986), SAI is located between 12°32'N and 81°43'W, ESE is found 16 nm south-east of SAI (between 12°24'N and 81°28'W), and SSW emerges 22 nm south-west of SAI (between 12°10'N and 81°51'W). There are about 300 fishers who regularly exploit the study area and represent a minority community of long tradition among the 60,000 inhabitants of San Andres Island.

Methods

Data used in this study was collected by technicians of the local management authority office of the Fishery and Agriculture Department from January 2004 to December 2006. During the study, an observer traveled daily to the 4 ports on San Andres early in the morning to register the number of boats present, assuming any missing vessels were out fishing. This information was used to estimate effective boat activity and the actual number of fishing trips.

The total fish landings and the large pelagic landings were randomly sampled 12 d of each month at each of the 4 ports where artisanal fishers sell their products, including North End, Cove Sea Side, San Luis and Newball Avenue. At each site, number of boats using handline gears remained similar throughout the study, with North End supporting the majority (50%), San Luis 24%, Newball Avenue 14% and Cove 12%. Fishers clearly identified the reef origin of their captures making it possible to couple spatial variability with the landing data.

During sampling days, between 80 and 100% of the active fleet were sampled. On each inspected boat, data on total landings were obtained using 15 or 50 kg portable weights, registering each pelagic species separately. In addition, every captain was interviewed to obtain information on fishing effort. Questions pertained to the trip duration, effective fishing hours, number of active fishers,

the type of fishing gear used and the area visited. Because most boats fishing for large pelagics are similar in structure and use similar fishing techniques, fishing effort was standardized to one fisher and one day. Another 43 older fishermen were interviewed to collect information on social perspective and complementary traditional knowledge.

A total of 377 specimens were measured (total length) to the nearest centimeter to determine the size frequency distribution for the most common large pelagic species. A plot of the size distribution referred to the length at first maturity (L_m) to establish the proportion of juveniles being caught at the species level. Information on L_m was obtained from previous isolated studies and published on-line information as follow: for blackfin tuna (Garcia-Cagide et al. 1994); for skipjack tuna (Collete and Nauen 1983); for wahoo (Brown-Peterson et al. 2000); and for dolphinfish (Oxenford 1999). The species identifications were based on the International Standard Statistical Classification of Aquatic Animals and Plants (FAO 2005).

A sample of 2,019 landings was then extrapolated to total landings using daily boat activity registry but CPUE was estimated for every fishing trip and species considered within the large pelagic group. To determine differences in mean CPUE by year and fishing zone, descriptive statistics were calculated and a one-way ANOVA was completed with Minitab™ (vers. 13.1), following verification of the test assumptions. If a significant F-value was estimated, a HSD-Tukey multiple range test ($P < 0.05$) identified homogeneous groups and temporal patterns in fish landings by month and year.

RESULTS

The Fishers and Their Fishing Activities

From the 300 active artisanal fishermen using the southern section of the Seaflower MPA, 71.2% predominantly used handlines, while the remaining 28.8% were free divers. Ages of fishers ranged from 30–50 yrs old, with the free divers in the younger age classes. Many fishermen were raised fishing alongside their fishermen fathers and have learned the skills from childhood. Progressive changes in fishing techniques were visible 30 years ago with the replacement of wooden boats with fiberglass boats and outboard engines replacing traditional sails. In contrast, the fishing gear has not exhibited significant changes during the same time period.

A regular fishing trip may use a handline or free diving, although the time dedicated is usually dependent on the location, weather conditions and the fisher's age. During this study, the handline fleet was comprised of 65 boats in 2004, 76 in 2006. On average, fishing boats are

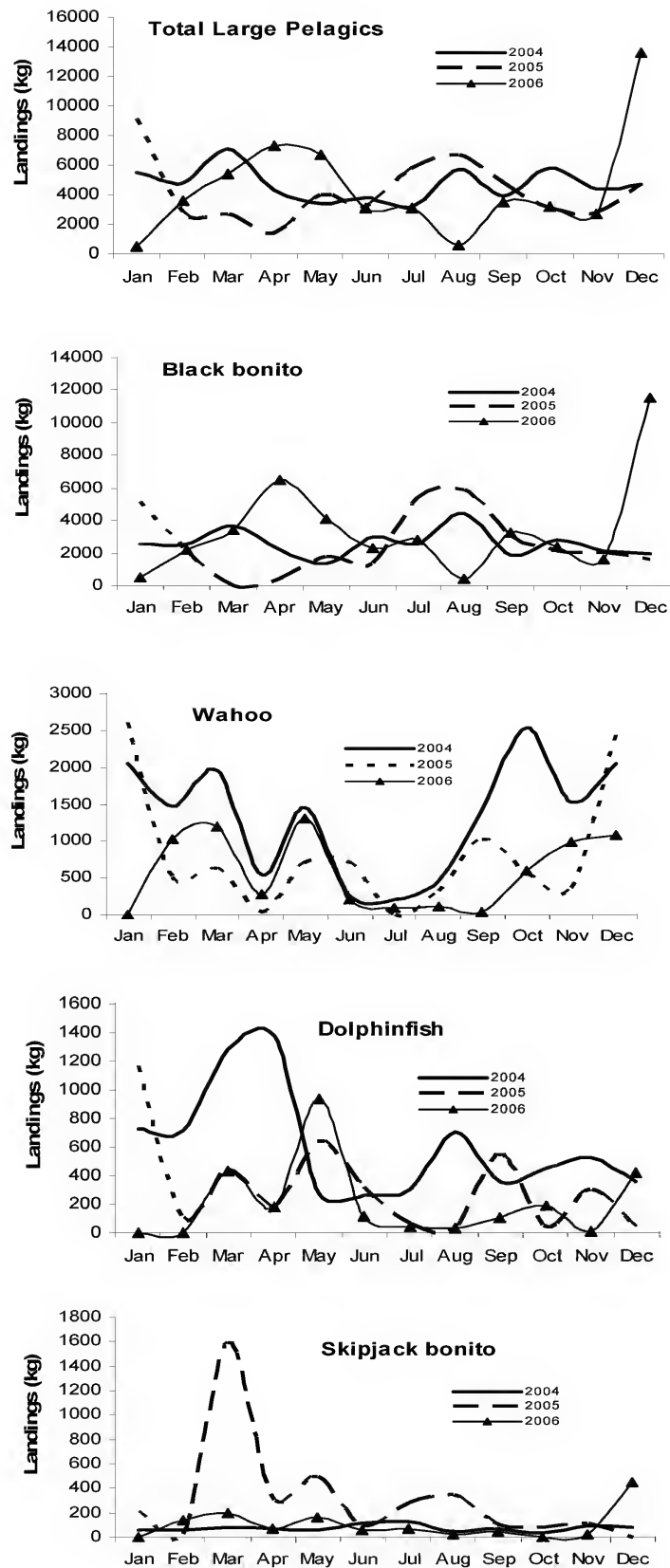


Figure 2. Monthly variation in large pelagic landings from the artisanal fishery in the southern section of the Seaflower MPA between 2004–2006.

TABLE 1

Estimated landings (kg) of the large pelagic fishes in the southern section of the Seaflower MPA discriminated by species and year.

Group	Scientific name	Common name	2004	2005	2006	Total
Offshore	<i>Thunnus atlanticus</i>	Blackfin tuna	31,219	30,884	41,058	103,161
	<i>Katsuwonus pelamis</i>	Skipjack tuna	890	3,663	1,224	5,777
	<i>Thunnus obesus</i>	Bigeye tuna	627	88	1,208	1,923
	<i>Makaira nigricans</i>	Black marlin		1041		1,041
	<i>Euthynnus alletteratus</i>	Little tunny	141	462	158	760
	<i>Thunnus albacares</i>	Yellowfin tuna		617		617
	<i>Auxis thazard</i>	Frigate tuna			4	4
Coastal	<i>Acanthocybium solandri</i>	Wahoo	15,941	9,906	6,949	32,797
	<i>Coryphaena hippurus</i>	Dolphinfish	7,344	3,889	2,459	13,693
	<i>Scomberomorus cavalla</i>	Sierra	502	462	134	1098
	Total		56,664	51,012	53,194	16,0871

7 m long (range 3 to 9 m) and propelled by one outboard engine between 40–75 HP. Fishermen leave early in the morning (04:00 to 06:00), commonly with 2 fishermen per boat. First they fish for bait and then troll for large pelagics for the remainder of the day. After trolling, some fishermen move to shallower waters in search of additional demersal catches. Handline test varied between 60 and 250 kg depending on the species. Usually, fishing for offshore pelagic species uses fresh blackfin tuna meat as bait, while coastal species utilizes homemade lures with 2 fish hooks and green or yellow phosphorescent trimmers. Species such as black marlin, wahoo, bigeye tuna require large hooks (00, 2, 3), and species such as blackfin tuna, skipjack tuna, dolphinfish are caught with smaller hooks (5, 6).

The catch is immediately eviscerated and stored under/between the boat seats or inside an ice box. Upon arrival to the port, the product is sold to small scale business men who begin a trade chain through the local restaurants, stores and general community. Only a small fraction of the total catch is actually bought by the fishing cooperatives. The price is fixed and determined annually by the government and classified into 2 categories: 1) red fishes consisting of snappers, groupers and wahoo with high market value, and 2) black fishes, consisting of barracudas, blackfin tuna, jacks, wave runner, trigger fish, grunts and others with lower market value.

Large Pelagic Fish Composition and Landings

It was estimated that large pelagic landings totaled 56,664 kg in 2004, 51,012 in 2005 and 53,194 in 2006. These captures represented on average 51% (\pm 5.6 standard deviation; SD) of the total artisanal landings. The large pelagic fish community was comprised of 8 spe-

cies belonging to 3 families (Scombridae, Coryphenidae and Istiophoridae) (Table 1). The blackfin tuna (*Thunnus atlanticus*) dominated the landings and accounted for 55% of the catch in 2004, 61% in 2005 and 78% in 2006. The second most abundant species was wahoo (*Acanthocybium solandri*) comprising 28%, 19% and 13% of the annual large pelagic landings, respectively.

There were no clear patterns in the monthly variation of large pelagic landings. In fact, the largest peak found in December 2006 of 13.6 m-ton was not consistent with patterns in previous years because maximum landings in 2004 occurred in March 2004 with 7.0 m-ton and in January 2005 with 9.1 m-ton (Figure 2). The 2006 peak was influenced largely by blackfin tuna landings (11.5 m-ton), a species which also contributed to the maximum landings in 2004 and 2005. However, maximum landings in March 2004 and January 2005 also included significant proportions of wahoo and dolphinfish (Figure 2). Temporal variation in landings for the most common species allowed identification of additional patterns (Figure 2). For example, blackfin tuna peaked in June–August, while wahoo had a primary peak in November–January and secondary peaks in April and July–August. Moreover, dolphinfish landings peaked from February–May and skipjack tuna peaked in March, with a secondary peak in June–July. Interestingly, the peak of skipjack tuna landings noted in March 2005 of 1.59 m-ton coincided with an absence of blackfin tuna landings. Abundance of this species was low in all other months and years, not exceeding 0.4 m-ton.

It was found that the large pelagic fish community was caught predominantly around SAI with decreased landings with distance from home port. During this study, captures from SAI accounted for up to 50.2% and decreased to

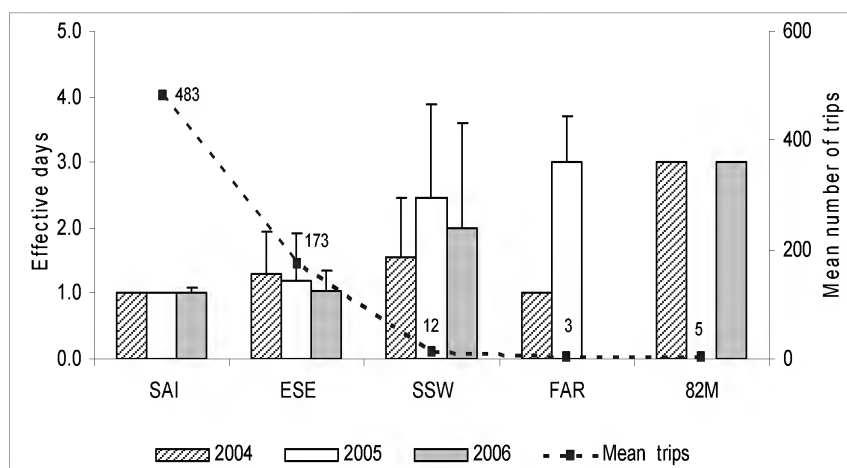


Figure 3. Variation in the mean number of effective days for the large pelagic artisanal fishery in the southern section of the Seaflower MPA. Errors bars indicate one standard deviation. Values on the secondary plots are the total number of trips at each fishing zone. See geographic locations of the fishing zones in Figure 1.

45.4% in ESE (16 nm from SAI), to 3.5 % in SSW (22 nm from SAI), to less than 1% in FAR and 82M (35–45 nm from SAI). Only at the 3 most distant reefs are landings still comprised of reef associated fish species, a result that is related to greater fishing effort exercised around SAI (Figure 3).

Catch Per Unit Effort (CPUE)

Mean values of CPUE were lowest around SAI, despite the significant landings and fishing trips, with values comparable to those distant areas supporting minimal effort targeting large pelagics (Figure 4). Higher values in CPUE were found in ESE and SSW with a mean of 12.5 kg/fisher-day (± 11.0 SD) and 9.2 kg/fisher-day (± 7.8 SD), respectively. The highest mean CPUE value found at the medium distance fishing grounds around ESE was indeed significantly different from CPUE value found around SAI ($F = 101.33$, $P < 0.001$). Due to the minimal data entries from distance reefs (FAR and 82M), data from these locations were excluded from the One-way ANOVA.

Pooling CPUE by year showed that 2006 had the highest values with a mean of 8.5 kg/fisher-day (± 9.9 SD) followed by 2004 data with 8.2 kg/fisher-day (± 7.3 SD) and 2005 with 7.3 kg/fisher-day (± 9.1 SD). These mean landings data differed significantly ($F = 3.17$, $p = 0.042$), with 2006 landings being >2005 but not 2004 nor was 2005 different than 2004 landings.

Length Frequency Distribution of Common Species

The large pelagic artisanal fishery in the southern section of the Seaflower MPA is extracting individuals below their length at first maturity (L_m) compared with published values, but the degree of juvenile proportions being caught

varies depending on the species (Figure 5). In the case of blackfin tuna, juveniles comprise up to 75.3% of the landings, while wahoo and dolphinfish represent 17.9% and 8.3% of the juvenile population, respectively.

DISCUSSION

Results presented here illustrate how the large pelagic fish group around the southern section of the Seaflower MPA experienced slight but progressive reductions in mean CPUE during the 3 years of collected data which affected each reef differently. For instance, species captured in SAI with the highest landings also resulted in low CPUE values, while medium distance reefs (ESE and SSW) appear to have highest CPUE. The most distant reefs are not important sites for large pelagic fishes, but are for reef associated species. In fact during the study, large pelagics did not exceed 2% of the total landings in FAR or 82M. A distance gradient appears to exist, but it was not clear as higher landings could have shifted from the closer reefs to medium distance reefs, as the former showed reduced catches. Therefore, the initial hypothesis was not fully tested.

Fishing zones in the southern reefs are likely experiencing a serial depletion phenomenon, obligating fishers to travel further to maintain similar catch levels and still make a profit. This progressive depletion can be seen in the case of the blackfin tuna, the most abundant species in the landings with more than 70% caught as juveniles. However, the presence of additional large pelagic species in the fishery (wahoo, dolphinfish, etc.) may also explain why this fishery has not yet completely crashed.

Figure 4. Variation in mean CPUE of the large pelagic fish groups at the Southern section of the Seaflower MPA. Error bars are 95% Tolkey HED confidence intervals.

Based on fishermen's traditional knowledge, fishing around SAI was dominated by reef associated stocks which were depleted in about 15–20 yrs. Fishing communities then redirected their effort to pelagic species. Now, 10 yrs later and with an increased effort to target those communities, the pelagic stocks is being significantly reduced. The depletion phenomenon observed around SAI may now be appearing at multiple distance reefs and threaten more distant reefs.

The status of the large pelagic fish stocks in the archipelago is still unknown, as well as their spatial and

temporal dynamics. Therefore, it is unclear exactly what is contributing to the low abundances observed. However, the results presented provide baseline information needed to determine the effectiveness of the recently established Seaflower MPA. Results also illustrate how primitive gear can still produce a severe reduction in abundances of several stocks, particularly when exploiting remote, small and isolated stocks. This is especially important because of the progressive increases seen in fishing effort through time. In fact, the number of regular fishermen in the 1970s were only 45 (Castro 2003) and this increased to 300 in 2006 (Table 2). Similarly, the number of handline boats were around 49 in 1995 (Castro 2003) and by 2006 there were 75 registered.

In addition, negative trends can be associated with the extraction of juvenile individuals of several pelagic species. Unexpected results showed how higher proportions of juveniles are taken from offshore environment (up to 76% for blackfin tuna and skipjack tuna) than the coastal zone (18% for wahoo and 4% for dolphinfish). It may be possible that areas around the southern reefs serve as juvenile habitats, but theory has not yet been investigated. Another unexpected result was the peak of skipjack tuna landings in March 2005. Although we do not know why this occurred, it is also noted that a similar peak for the species occurred between January and February 1995. Landings in 1995 were similar to those in 2005 with 3.2

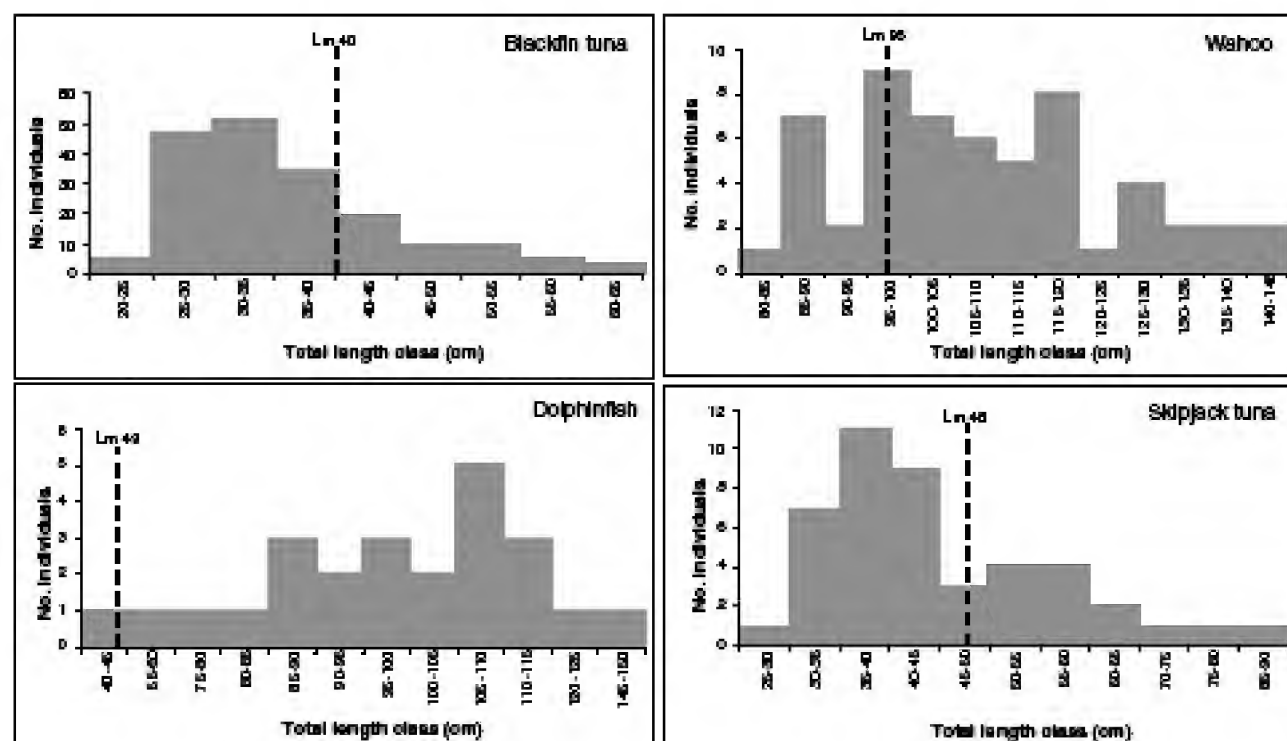


Figure 5. Length frequency distributions for the most abundant coastal and offshore pelagics. The dash line indicates length at first maturity (L_m).

TABLE 2

Progressive increases in artisanal fishing effort fishing at the Archipelago southern reefs. Data taken from Pomare 1999 and Castro 2005.

Year	No. fishermen	No. of handline boats
1972	45	—
1980	170	—
1984	128	—
1994	163	—
1995	—	49
1997	206	—
2001	—	61
2002	225	—
2005	—	65
2006	300	75

m-ton and represented 66% of the total landings for that year (Pomare 1999).

Despite previous results, there is a general perception that pelagic species are less vulnerable to over-fishing and therefore there is no need to implement stricter fishing regulations. Given this, local managers face a difficult situation reversing the negative trends while mediating increasing fishermen conflicts, and the deterioration of their quality of life. The long term expected MPA benefits and alternative economical activities should be carefully explored. Perhaps, with the integration of existing initiatives and regional programs focused on management of the large pelagic fisheries, such as those of the Caribbean Community Countries (CARICOM), the International Commission for the Conservation of Atlantic Tunas (ICCAT) and the Western Central Atlantic Fisheries Commission (WECAF), there is potential for the evaluation and subsequent recommendation for more appropriate management of these stocks. Good perceptions and positive changes in abundance, as well as better understanding and management policies are possible only if they properly address the biology of the species and the components of its complete life cycle (Mahon and McConney 2004).

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Sandra Grant

University of Manitoba

Fikret Berkes

University of Manitoba

Johnson St. Louis

Ministry of Agriculture, Lands, Forestry and Fisheries, Grenada

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A HISTORY OF CHANGE AND REORGANIZATION: THE PELAGIC LONGLINE FISHERY IN GOUYAVE, GRENADA

Sandra Grant,^{1*} Fikret Berkes,¹ and Johnson St. Louis²

¹Natural Resources Institute, University of Manitoba, 70 Dysart Road, Winnipeg, Manitoba, R3T 2N2 Canada, Phone (204) 474-8873, Fax (204) 261-0038. *E-mail linegrant@gmail.com

²Fisheries Division, Ministry of Agriculture, Lands, Forestry and Fisheries, Botanical Gardens, St. George's Grenada

ABSTRACT This paper traces the history of the pelagic surface longline fishery in Gouyave, Grenada, noting 4 major periods of change from pre-1985 to 2004. Reconstructed from document reviews, newspaper articles, oral history, and key informant interviews 1) the pre-1985 period was the time when the longline was introduced and popularized by the Cubans, 2) the period of institutionalization and technology development (1986–1990) corresponded to the strengthening of institutional arrangements and the initial improvements in technology, 3) the Coastal Fisheries Development Project (CFDP) of 1991–1999 was the period of international donor support and further technology change in longline construction, and finally 4) the 2000–2004 period marked innovation, training and fish quality control for export markets. The main point of the paper is that fisheries management is about the management of change. Fishery managers need to learn to deal, not only with technology change, but also with surprise and variability related to biophysical change (e.g., hurricanes), change in markets, and other external drivers such as international policies. Key considerations for managers to deal successfully with change include: learning from experience, capacity building, and the need to engage cooperatively with fishers and communities, the private sector, and non-governmental organizations.

RESUMEN Este documento relata la historia de la industria pesquera del palangre de superficie para la captura de los pelágicos basada en Gouyave, Grenada, señalando 4 periodos principales de cambio entre 1985 hasta 2004. Elaborada mediante la revisión de documentos, artículos de periódico, relatos orales y entrevistas de los informantes claves: 1) el periodo anterior a 1985 cuando el palangre fue introducido y popularizado por los Cubanos, 2) el periodo de la institucionalización y desarrollo de la tecnología (1986–1990) correspondiente al fortalecimiento institucional y los inicios en el mejoramiento tecnológico, 3) el Proyecto de Desarrollo de la Pesca Costera (CFDP) de 1991–1999 fue el periodo de la apoyo internacional por parte de los donantes y un mayor cambio en la tecnología fabricación de los palangres, y finalmente 4) el periodo del 2000–2004 que marca la innovación, el entrenamiento y el control de calidad del pescado para los mercados de la exportación. El punto principal de este trabajo es si el manejo de las pesquerías tiene que ver con el cambio en su manejo. Los gerentes pesqueros necesitan aprender a manejarse no solo con cambios en la tecnología sino también con la sorpresa y la variabilidad relacionadas a cambios biofísicos (ej. huracanes), cambios en los mercados, y otras fuentes externas tales como políticas internacionales. Consideraciones claves para que los gerentes se puedan manejar exitosamente, incluido los cambios: aprendiendo de la experiencia, capacidad institucional, y la necesidad de comprometerse de manera conjunta con los pescadores y las comunidades, el sector privado y las organizaciones no gubernamentales.

INTRODUCTION

A fishery often undergoes changes in response to various factors: biological (e.g., resource availability), economic (e.g., market demand), and political (e.g., changes in resource management policies). Many of these changes are unpredictable and/or beyond the capabilities of the resource manager, as discussed, for example, by Charles (2001) who refers to the 'illusion of certainty' and the 'fallacy of controllability' in fisheries management. Even though the conventional philosophy of management is based on a tradition that assumes predictability and control, our ability to actually predict ecosystem behavior and resource use trajectories are limited, and models based on equilibrium thinking often do not work (Wilson 2006).

Marine ecosystems on which fisheries are based are complex adaptive systems characterized by constant change and multiple equilibria (Levin 1999; Gunderson and Holling 2002). They are subject to natural disturbances (e.g., hurricanes), changes originating from within the system, and to external drivers created by human actions, as increasingly recognized by global studies such as the Millennium Ecosystem Assessment (MA 2005). If fisheries are complex systems, then fishery problems need to be treated as a complex system problem. As such, management processes cannot follow blueprints; rather, they should be adaptive and flexible, able to deal with uncertainty and surprise, involve partnerships to deal with issues at different levels of organization, and build capacity to adapt to change (Berkes et al. 2001).

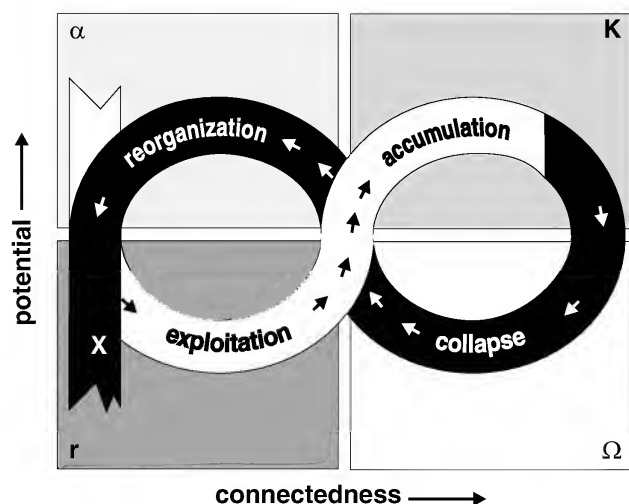


Figure 1. The adaptive renewal cycle. The cycle reflects changes in 2 properties: y-axis, the potential that is inherent in the accumulated resources and structure; x-axis, the degree of connectedness among controlling variables. The exit (marked with an X) from the cycle indicated at the left of the figure suggests, in a stylized way, the stage where the potential can be leaked away and where a shift is most likely into a less productive and organized system. The shaded part of the cycle is termed the 'backloop' and concerns the release and reorganization phases (modified from Holling 2001, Gunderson and Holling 2002). Terms of the adaptive cycle are: exploitation (r) period; accumulation (K) period (termed conservation phase by Holling 2001); collapse (Ω) period (termed release in Holling 2001) and reorganization (α) period called the 'back loop'.

In this paper we use the resilience approach and the idea of adaptive renewal cycles to analyze the change in a Caribbean fishery. As proposed by Holling (2001), the heuristic model of the adaptive renewal cycle consists of 4 phases (Figure 1). It starts with an exploitation (r) phase, followed by accumulation (termed conservation phase K, by Holling 2001). This 'front loop' is followed by a collapse (termed release phase Ω) and reorganization (α) period, called the 'back loop.' The front-loop coincides roughly with the period of growth and development of a fishery. The back-loop, often neglected in resource management, is usually triggered by a disturbance and tends to occur over a short time period. The adaptive renewal cycle can provide insights into the response of fisheries to environmental, social, and economic change, as illustrated by cases in Florida (Gunderson et al. 2002) and southern Brazil (Seixas and Berkes 2003).

As we show with our Caribbean fishery case, the back-loop raises important considerations in resource management (Berkes et al. 2003). The back-loop is a time for both crisis and renewal, and provides a fertile environment for experimentation. It is often this 'window of opportunity'

created by collapse and reorganization that shapes the subsequent developments in a resource system (Holling 2001, Gunderson and Holling 2002). In approaching the phenomenon of change in a complex world, the resource manager needs to consider a range of factors—ecological, social, technological, and other (Plummer and Armitage 2007). Hence our unit of analysis in this paper is not the ecological system by itself or the social system by itself, but the fishery as an integrated social-ecological system (Berkes and Folke 1998).

The objective of this paper is to analyze how the pelagic surface longline fishery in Gouyave, Grenada, deals with change. We use the Holling adaptive renewal cycle to examine change as technological, social, and institutional innovation in what we assess to be 4 cycles in the Gouyave fishery. The paper highlights changes in behavior, activities, and knowledge in maintaining a viable fishery by conserving sufficient memory (information, knowledge and experience) to allow for innovation, learning, and reorganization. We conclude by drawing lessons from the case and finding 3 characteristics of managing change.

STUDY AREA AND METHODS

Study area

Grenada is an island in the Eastern Caribbean, between 11°00' and 12°30' north latitude, with a total area of 311 km² (Figure 2). The town of Gouyave, in the parish of St. John's, is located on the west coast of the island about 19 km north of St. George's town. The estimated population in Gouyave is 2,100 about 2% of the national population. Of the estimated 2,200 fishers in Grenada, over 300 operate from Gouyave, and most of these (82%) are involved in longline fishing. These fishers operate 100 active longline fishing vessels of 3 types. The first, open pirogues, are semi-decked, wooden, 5–7 m in length, powered by a single 15–40 HP outboard engine, and equipped for multiple-purpose fishing. The second, cabin pirogues, made from wood and/or fiberglass are 7–9 m in length, powered by two 40–75 HP outboard engines, and equipped for longline fishing. Third, launchers, made from wood and fiberglass are 9–15 m in length, powered by a 130–300 HP inboard diesel or gas engine, and equipped for overnight fishing. Longline fishers target pelagic species including yellowfin tuna (*Thunnus albacares*), white marlin (*Tetrapturus albidus*), blue marlin (*Makaira nigricans*), common dolphin (*Coryphaena hippurus*), sailfish (*Istiophorus albicans*), swordfish (*Xiphias gladius*), wahoo (*Acanthocybium solandri*), bigeye tuna (*Thunnus obesus*), and blackfin tuna (*Thunnus atlanticus*).

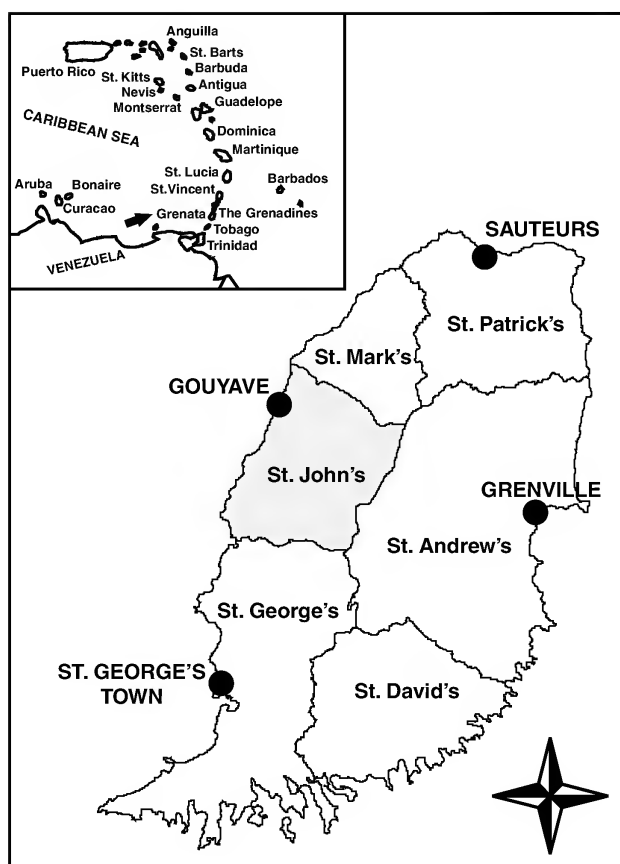


Figure 2. The study area of Grenada and the Eastern Caribbean.

Methods

The history of the surface longline (or simply longline) fishery was reconstructed and documented through literature/document review, newspaper review, oral history, and key informant interviews. Literature and documents were gathered from government correspondents, libraries, and newspaper articles dating back to the 1980s and were provided by Osmond Small, the former President of the St. John's Fishermen Association. An oral history technique was used to gather information on the history of fishing in Gouyave. Twelve key individuals provided detailed information on the history of the longline fishery, marketing, and roles and activities of the Fisheries Division. Research findings from the literature and document reviews were supplemented with oral history and interviews to check for consistency. Following Hurricane Ivan which destroyed the island's infrastructure in September 2004, the researcher returned to the island in April 2005 to gather information on how the fishery reorganized after the crisis. This was accomplished with semi-structured interviews conducted with community members, fishers, the Grenada Community Development Agency (GRENCODA; a local non-governmental organization), and staff of the Fisheries Division.

RESULTS

We traced the history of the pelagic fishery based on 4 time periods (Figure 3). The first, the pre-1985, was the period when the Cuban longline technique was introduced. The second, institutionalization and technology development during 1986–1990, was the period of strengthening institutional arrangements and the initial improvement in longline fishing technology. The third, the Coastal Fisheries Development Project (CFDP) between 1991 and 1999, was a period of further donor support and technological changes in line construction. Finally, the period from 2000–2004 was a time of technological innovation.

Pre-1985 period

Traditionally, fishers in Gouyave used the '3-line' fishing (handline technique) to catch pelagic fish. By the early 1970s, observations of the effectiveness of the longline techniques used by illegal vessels led fishers to design and experiment with this gear (Grant and Baldeo 2006). In 1979, the People's Revolutionary Government (PRG) embarked on a number of projects to improve fishing. They established the Grenada Fisheries Training School in True Blue St. George's with technical assistance from the Government of Cuba, where students were trained in pelagic fishing techniques (longline, pole and line, gillnet) and gear construction. The Grenada Fisheries Company was also established to improve the harvesting of fish for domestic consumption. The company had a Fish Processing Plant to smoke, fillet, and salt fish for local and export markets and a National Fisheries Company to store and market wholesale and retail fish (J. St. Louis, per. comm., Fisheries Division, St. George's, 2003). To support local fisheries, the government encouraged the development of fishermen cooperatives (Sandford and Vigilant 1984).

The fishery grew steadily between 1980 and 1981 as production at the Fish Processing Plant increased from 18 kg/day to 1,588 kg/day, due mainly to the production of canned tuna and flyingfish in tomato sauce for the export market and fillets and smoked fish for the local market (Aberdeen 1982). By 1982, the fishery started showing signs of stress as problems with poor organization and management left the National Fisheries Company unable to cover expenses. Likewise, a world recession in 1980–1982 also reduced the demand for Grenadian goods (Aberdeen 1982, Sandford and Vigilant 1984).

In 1983, the United States (USA) invaded Grenada and in the process some fishing infrastructure (boats, agro-industry) were destroyed. Gouyave fishers who were attending the Fisheries Training School and working at

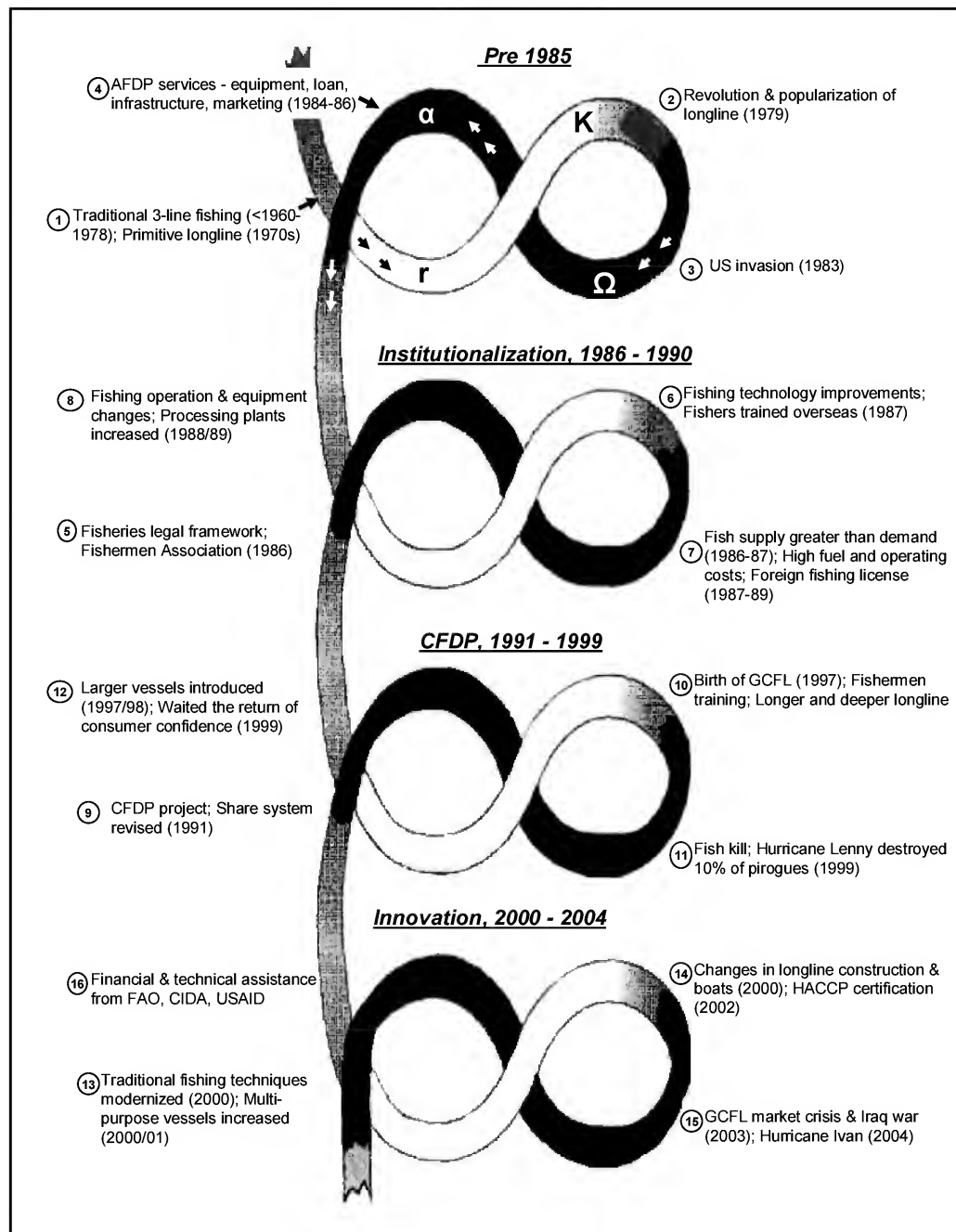


Figure 3. Timeline for the development of the longline fishery as represented by successive iterations of the modified adaptive cycle. The four found in the pre-1985 panel are defined in the Figure 1 caption.

the Fish Processing Plant returned to their communities to shape the local development of the longline fishery (J. St. Louis, pers. comm., Fisheries Division, St. George's, 2003).

The Artisanal Fisheries Development Project (AFDP; 1983–1985) that helped reorganize the fishery was funded by the World Bank International Fund for Agricultural Development (US\$2.7 million) and the Venezuelan

Investment Fund (US\$1 million), together with a counterpart contribution by the Government of Grenada (WECAFC 1985). The objectives were to develop infrastructure and improve technical and support services. Program activities included: selling imported fishing gear and equipment; operating a machine shop to service and repair engines; organizing a fish market program to distribute processed fish to buyers in Grenada; improving infrastructure to land, clean, weigh, and sell fish; improving data collection

system to handle vessel data and monitor gas rebates and duty free concessions; and introducing a line of credit for fishers, vendors, and boat builders.

Institutionalization and technology development 1986–1990

In 1986, the most comprehensive fisheries legislation to date (the Fisheries Act #15 of 1986), was enacted. With this Act and the Fisheries Regulation #9 of 1987, the Chief Fisheries Officer was able to organize a Fisheries Division. That same year, staff at the AFDP administrative office were transferred to the Fisheries Division. By 1988, the Fisheries Division was a fully functioning body with administration, biology, technology, aquaculture, extension services, and statistics units to provide services in licensing, concessions, enforcement, and data and information systems. By the end of 1990, the Fisheries Division was in local communities talking with fishers, dealing with conflicts, providing training in fishing technology and navigation to further developing the fisheries (J. Finlay, pers. comm., former Chief Fisheries Officer, St. George's, 2003).

During this period, fishers launched the St. John's Fishermen Association (SJFA) in Gouyave with a US\$100,000 loan from the Humanistisch Instituut Voor Ontwikkelings Samenwerking (HIVOS) through the Agency for Rural Transformation. This loan financed the building of a gas station to sell marine fuel, a tackle shop to sell fishing equipment, and a meeting room for fishers (O. Small, pers. comm., former president of the SJFA, Gouyave 2003). The objectives of the SJFA were to retail fishing tackle and equipment, to process and market fish, to improve the quality and output of fish products, to assist members in seeking financial assistance, and to make recommendations to government on matters relating to the fishery (SJFA 1986). The success of the SJFA led to the formation of the National Fishermen Association in 1990, an umbrella organization which worked towards improved conditions for fishers (O. Small, pers. comm., Gouyave 2003).

Capacity building included longline training provided by the Fisheries Division and overseas fishing training in Japan, Korea, and Canada to help fishers apply new knowledge to existing technology. Subsequently, twisted monofilament line was replaced with single monofilament line, and a box used for the deployment of longline was replaced with reels (Samlalsingh et al. 1999, Grant and Baldeo 2006).

Problems came with improvements in longline technology. First, these improvements resulted in the growth of the fishery; a 73% increase in pelagic fish landing in 1986

over 1984 figures (Fisheries Division landings statistics). Landings were so large that Gouyave fish market could not store excess fish; thus, fishers were forced to bury some of the catch. Second, high fuel prices increased operating costs (pirogues with two 75 HP engines consumed 38 liters of fuel per trip) which forced fishers to think about alternative boat and engine options (R. Gill, pers. comm., fisher, Gouyave, 2003). Third, the government granted fishing licenses to foreign operators with advanced skills and expertise who marketed their catch outside of Grenada and evaded the government's fee of EC\$0.25 (1 US\$ = 2.71 EC\$) per kg of fish caught (Grenada Guardian, 2 December 1988).

To deal with excess fish, the government, fishers, and the private sector found options to increase fish sales and reduce operating expenses. In Gouyave, the NORDOM Seafoods Ltd. processing plant became operational and focused on the export of pelagic fish to the USA (N. Simon, pers. comm., NORDOM Seafoods Ltd., Gouyave, 2003). In St. George's, the AFDP processing plant and the Caribbean Seafoods Ltd. (a privately owned company) processed fish for local and export markets (Weidner et al. 2001). The solution to high operating costs was to replace the 75 HP engines with more efficient 40 HP ones (R. Gill, pers. comm., fisher, Gouyave 2003). The problem of foreign operators was solved when the National Fishermen Association launched a series of protests to pressure the government to stop issuing foreign licenses (Informer, 20 January 1989).

The Coastal Fisheries Development Project (CFDP) 1991–1999

The fishery entered another period with larger boats, modern longline equipment, loans to fishers, and improved infrastructure with support from the Coastal Fisheries Development Project (CFDP). The CFDP was a grant aid cooperation project between the Governments of Grenada and Japan valued at US\$4.68 million. The project aimed to introduce large-size fishing vessels to exploit offshore resources and to consolidate support services by improving the fishery environment and distribution facilities. The government received eight 11 m longline fishing vessels, accessory supplies and longline material, 4 vehicles for extension including 2 insulated trucks for transporting fish, and tools and equipment for gear repair facilities. Gouyave benefited from this project with the construction of a fishermen's centre with a small jetty, block ice and plate ice-making machine, cold storage facilities, lockers, and other equipment (J. Finlay, pers. comm., former Chief Fisheries Officer, St. George's, 2003).

During this period the foundation for future growth was laid. First, the goal of Gouyave fishers was to fish further offshore with minimum capital and operational expenses. They considered Japanese longline vessels too expensive to own and maintain, hence designed an economical offshore vessel (or launcher) with an inboard diesel engine. The prototype was built in the USA, and by 1997 a 12 m vessel with sleeping quarters, specific to Gouyave needs, was fully operational (N. Simon, pers. comm., NORDOM Seafoods Ltd., Gouyave 2003).

Second, boat owners further reduced operating costs by changing the share system. Traditionally, income from fish sales was divided into 3 parts: one for the boat and 2 for crew. The boat's share included all expenses and the owner's share. But with high operating expenses, many boat owners could not make a profit. With the new share system, expenses were deducted first and the remainder divided in two, one part for the boat and one part for crew (R. Gill, pers. comm., fisher, Gouyave, 2003).

Finally, continuous capacity building was critical to the survival of the fishery. With an increase in offshore fishing, the Fisheries Division provided captaincy training for Gouyave fishers. Such training included fisheries conservation and laws, safety at sea, navigation, Global Positioning System education, and seamanship and boat handling. Also, as longline technology developed, the Fisheries Division provided technical assistance in collaboration with regional and international organizations.

Improved fishing vessels and equipment, access to fishing loans, capacity building, and a thriving export market resulted in the growth of the fishery. Boat size increased from 7 m in 1979 to 12 m by 1997, and longlines were built longer and deeper, from 46 hooks in 1983 to over 250 in the late 1990s. Landings from the longline fishery peaked between 1993 and 1995 at 474,000 kg. To deal with increased landings, the AFDP processing plant was transformed to the Grenada Commercial Fisheries Limited (GCFL) in 1997. The company processed fish fillets, steaks, and salted shark for local and export markets. They also purchased fish directly from Gouyave fishers and transported it by insulated trucks to St. George's (Weidner et al. 2001).

In late 1999, the fishery in Gouyave declined due to a series of events. Extreme storm surges, a direct result of category 4 Hurricane Lenny hit the west coast of Grenada in November 1999. The storm surge was accompanied by dangerous waves and flooding of 3–5 m above normal tides (McConney 2003) which damaged coastal roads, homes, and the jetty. In Gouyave, fishing boats and equipment were destroyed, including 10% of the cabin pirogue fleet. The estimated cost to local fishers and vendors was

US\$189,557 (Jessamy and Turner 2003). Also in 1999, a fish kill in the southeastern Caribbean caused by the bacterial agent *Streptococcus iniae* and poor water quality resulted in significant death to demersal reef fish (Ferguson et al. 2000, Willoughby et al. 2002) which led to a decline in fish consumption. Thus, by the end of this period landings were down to 100,000 kg (Fisheries Division fish landings data).

To reorganize, the government and other organizations provided financial assistance to fishers. In 1999–2000 GRENCODA applied to the Canadian International Development Agency (CIDA) and received grants of US\$15,000 to help rebuild the fishery in Gouyave (GRENCODA 2000). Many fishers used the financial assistance from the government and GRENCODA to re-invest in open pirogues. They evaluated distance traveled, economic return, safety of the vessel, and capital investment of open versus cabin pirogues and decided open pirogues were more economical (C. Richards, pers. comm., Gouyave fish market, 2003).

Innovation 2000–2004

Storm surges, rough seas, decline in fish catches, increasing numbers of fishers, and indebtedness to the bank were factors that forced fishers to change fishing operations and strategies once again. Business practices changed from boat owner/investor dominated operations, to crew members purchasing boats to become a new class of owner/captain. The 6-month fishery was extended to a year as fishers diversified their activities by altering existing longline technology and modernizing traditional fishing techniques. One such innovative technique was the modified longline specifically constructed to catch blackfin tuna (Grant and Baldeo 2006).

Overnight, offshore fishing, diversification, modernized techniques along with further technological innovations increased fish catch in Gouyave to over 500,000 kg in 2001. To further increase fish export to regional and international markets (particularly Europe), Fisheries Division and Ministry of Health developed a program to ensure that all fish products met European Union and other fish health safety standards. The agencies enacted legislation to ensure Hazard Analysis and Critical Control Point (HACCP) and Sanitation Standards and Operating Procedure (SSOP) standards at processing plants, trained 350 individuals in fish processing standards, and set up a testing laboratory (J. St. Louis, pers. comm., Fisheries Division and F. Balwant, pers. comm., Ministry of Health, St. George's, 2003). By 2002 all 5 fish processing plants in Grenada received HACCP compliance status, and 2 were certified to export fish to the European Union.

However, a series of events caused the fishery to decline again. In January 2003, GCFL experienced economic hardship and by March (the peak month for pelagic landings) fishers had to reduce fishing. Later that year, the war in Iraq caused overseas buyers to reduce fish prices. September 7, 2004 Hurricane Ivan caused damage to boats, equipment, engines, fishing gear, safety equipment, communication facilities, seines, and fishing infrastructure valued at over US\$2,115,000 (Government of Grenada 2004).

Reorganizing after the hurricane, the community spent the first 3 days replacing roofs, clearing roads, and removing debris then later focused on the fisheries sector. Compared to the rest of Grenada, the fishery in Gouyave received little damage to fishing vessels because past experiences with storm surges and tropical storms had taught fishers how to secure their equipment. However, low quantities of bait, rough seas, and strong currents hindered longline fishing activities. As soon as roads were cleared and air transportation resumed, NORDOM Seafoods Ltd. exported the first batch of fish a month after Hurricane Ivan. By November 2004, the Fisheries Division was able to secure financial and technical assistance for short- and medium-term support to rebuild the fisheries. The Government, the Food and Agriculture Organization of the United Nations (FAO), and CIDA provided finances to refurbish, expand, and upgrade the Gouyave Fish Market; the FAO/CIDA gave special assistance to repair boats, replace engines and equipment; the FAO provided financial and technical support for a 24 hr ship-to-shore communication system; the USAID financed small grants to assist in the recovery and business reactivation; and GRENCODA/USAID provided financial assistance to replace engines and equipment (Government of Grenada 2004). National fish exports resumed 2 months later and by March 2005 the country was exporting up to 60% of fish landed (N. Simon, pers. comm., NORDOM Seafoods Ltd., Gouyave, 2005). Finally, the Agency for Reconstruction and Development (ARD) was established by the government as a monitoring and coordinating body to facilitate and implement long-term recovery and rebuilding processes following Hurricane Ivan.

CONCLUSIONS

The ability to deal with change, maintain options, and take advantage of 'windows of opportunity' in a resilience sense (Holling 2001, Gunderson and Holling 2002) is crucially important to the success of any fishery. The Gouyave case demonstrates how the pelagic longline fishery dealt with biophysical changes (including hurri-

canes and storms) and social changes related to technology (boats and gears), fishing activities (bait use, marketing), and management (policies, legislation).

We used the heuristics of the adaptive renewal cycle (exploitation, accumulation, collapse, and reorganization) to examine social-ecological change and identified 3 characteristics of managing change. First, managing change involves learning from experimentation and accumulated experience by building and conserving memory (information, knowledge) to allow for innovation, reorganization, and growth. Second, managing change also requires continuous capacity building; as the fishery evolved, new skills are required. Finally, managing for change depends not only on governments but the interactions of the fishers, the private sector, non-governmental organizations, and community members working together, with each providing specific strengths and roles.

Fisheries management and development is challenged by the complexities and uncertainties of social-ecological systems. Unpredictable changes include not only hurricanes but also military interventions, and the market demand may be further impacted by fish quality regulations and distant wars. Finally, changes such as those related to international regulations (Singh-Renton et al. 2003) are also in the 'unpredictable' category from a small island nation point of view.

Thus, the manager is limited in the scope of management-as-control. Rather, it appears that the role of the fishery managers is to guide the fishery to evolve in response to various drivers by encouraging learning and facilitating capacity building to take advantage of numerous 'windows of opportunity' (Berkes et al. 2003, Wilson 2006). Likewise, managers can guide partnerships by encouraging fishers, the private sector, government, non-governmental organizations, and community members to work together; as each has a role to play in a more comprehensive approach to fisheries management. This kind of approach is part of managing for change, and likely requires a skill set different than that for predictability and control.

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Whale Sharks of the Western Caribbean: An Overview of Current Research and Conservation Efforts and Future Needs for Effective Management of the Species

Rachel T. Graham

Wildlife Conservation Society, Belize

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WHALE SHARKS OF THE WESTERN CARIBBEAN: AN OVERVIEW OF CURRENT RESEARCH AND CONSERVATION EFFORTS AND FUTURE NEEDS FOR EFFECTIVE MANAGEMENT OF THE SPECIES

Rachel T. Graham

Wildlife Conservation Society, PO Box 37, Punta Gorda, Belize, E-mail rgraham@wcs.org

ABSTRACT Whale sharks (*Rhincodon typus*) are seasonal visitors to four sites in the Western Caribbean, 3 of which are encompassed by the Mesoamerican Barrier Reef. Predictable encounters with the world's largest fish have raised this species' profile globally and led to several research and conservation efforts that aim to elucidate the need for information for the species management and balance the growing demand for highly lucrative encounter tourism. Tagging studies have demonstrated that the whale shark population is relatively small and likely forms a single population. Individuals move throughout the region between 3 of 4 known feeding sites and are capable of timing their movements to pulses of productivity. Whale shark tourism's dramatic growth has led to a range of protective measures and scientific studies both precautionary and reactionary that require better harmonization throughout the region to be effective. This paper will provide an overview of the status of whale shark research and conservation efforts in the Western Caribbean and identify future management needs to minimize anthropogenic impacts and enable continued whale shark visitation at key feeding sites.

RESUMEN Los tiburones ballenas son visitantes estacionales a cuatro sitios en el Caribe occidental, tres de los cuales se ubican en el arrecife Mesoamericano. Encuentros previsibles con el pez mas largo del mundo han elevado el perfil de esta especie globalmente y ha llevado a la implementación de varios esfuerzos científicos y conservadores quienes tratan de dilucidar la demanda creciente y económicamente lucrativo por el turismo de encuentro. Estudios de marcaje han demostrado que la población de tiburones ballenas es relativamente pequeña y probablemente forma una sola población. Individuos se mueven a lo largo de la región entre 3 de 4 sitios conocidos de alimentación, mostrando una habilidad para sincronizar sus movimientos a pulsos de productividad. El desarrollo dramático del turismo de tiburón ballena ha llevado a la implementación de medidas de protección y estudios científicos de naturaleza precaucionarías y reaccionarias que requieren mejor armonización en la región para ser efectivos. Este artículo proveerá una perspectiva de conjunto de la situación de tiburón ballena en el Caribe occidental e identificara las necesidades de manejo futuras para ayudar en minimizar impactos antropogénicos y permitir que las visitas a los sitios alimenticios claves sigan siempre.

INTRODUCTION

Whale sharks observations are increasingly reported worldwide as greater attention is paid to the world's largest fish by tourists, the private and public sectors as well as scientists and conservationists. With its *K*-selected life history features of longevity, late maturation, relatively low fecundity, great size (up to 20 m total length) (Colman 1997), high mobility (Eckert and Stewart 2001, Wilson et al. 2006, Graham et al. 2007), site fidelity (Graham 2003, Graham et al. 2006) and docility, whale sharks are rapidly acquiring a reputation as ambassadors for the world's oceans. Science is rapidly catching up with increasing public attention paid to whale sharks and overturning common beliefs about a species once deemed obligatorily epipelagic and whose notoriety stemmed primarily from ship strikes (Gudger 1937, 1939). Consequently, new insights exist on population size and structure (Meekan et al. 2006, Graham and Roberts 2007), diving patterns (Graham et al. 2006), movements (Gunn et al. 1999, Eckert and Stewart 2001, Eckert et al. 2002, Graham 2003, Wilson et al. 2006, Graham et al. 2007) and site fidelity (Graham 2003,

Graham et al. 2006). This information complements that acquired on biology and reproduction (Joung et al. 1996, Clark and Nelson 1997), feeding behavior (Heyman et al. 2001), research methodologies (Arzoumanian et al. 2005, Graham and Roberts 2007) and tourism (Davis et al. 1997, Davis 1998a, Davis 1998b, Graham 2003, 2004).

In the Western Caribbean, the occurrence of predictable whale shark sightings has engendered a unique partnership of scientists, conservationists, fishermen and tour guides seeking to answer the same questions about the world's largest fish. However, the motivations of each stakeholder group in the region is different. Scientists quest for knowledge about the population size and behavior of a relatively little known but highly charismatic animal whereas conservationists view whale sharks as a means of generating enthusiasm and interest in marine conservation in general. The public sector utilizes whale sharks as a means of generating international goodwill for the conservation of a migratory—yet non-controversial or targeted marine species. The private sector and fishers view whale sharks as a lucrative and renewable source of tourism income. This paper aims to compile knowledge

gathered to date on whale sharks of the Western Caribbean and provide recommendations for the management of anthropogenic activities that may impact whale sharks and their prey. The recommendations are further applicable to other regions that host whale shark feeding sites.

SETTING AND BACKGROUND

The Western Caribbean region's whale shark aggregations

The Western Caribbean is bounded by Mexico's Yucatan Peninsula and Belize to the West, by Guatemala and Honduras to the south and Cuba to the north, an area that encompasses about 610,000 km². Sea-surface temperature varies little throughout the year (25–30°C) and primary productivity is relatively low (<175 gC/m²/yr)¹. The Caribbean current runs from east to west through the Yucatan straight into the Gulf of Mexico (GOM) becoming the Loop Current and eventually the Gulf Stream. The region forms a subset of the Caribbean Large Marine Ecosystem and encompasses the Mesoamerican Barrier Reef, the world's second largest after Australia's Great Barrier Reef. This site is identified as one of the world's hotspots for marine biodiversity (Roberts et al. 2002). The region is home to an estimated 6.4 million inhabitants, which is projected to grow by 0.2% to 2.3% by 2015². The expanding population's increasing pressure on marine resources either through extractive use such as fisheries or non-extractive use such as tourism can only exacerbate the demand placed on marine species.

The Western Caribbean possesses 4 known whale shark feeding sites with different biophysical characteristics (Figures 1 and 2). Whale shark sightings increase dramatically between February and May off the north shore of (1) Utila, Honduras, an area located at the edge of the Mesoamerican continental shelf break on the periphery of a documented counter-clockwise gyre³ that concentrates primary and secondary productivity. Although whale shark

feeding behavior and food choices have not been studied at this site, whale sharks are most often encountered feeding on pelagic sprat (*Clupeid* spp.) that are preyed on by schools of little tunny (*Euthynnus alletteratus*), skipjack, blackfin and yellowfin tuna (*Katsuwonus pelamis*, *Thunnus atlanticus* and *T. albacares*). In Belize (2), the whale sharks aggregate yearly to feed on the fertilized spawn of dog and cubera snappers (*Lutjanus jocu* and *L. cyanopterus*) (Heyman et al. 2001, Graham et al. 2006). Feeding on spawn occurs within the boundaries of the Gladden Spit and Silk Cayes Marine Reserve on the edge of a fore-reef slope that drops steeply to over 2,000 m into the southern finger of the Cayman Trench. Peak whale shark visitation occurs at Gladden Spit from March to June and again in August and September, periods associated with the lunar-entrained snapper spawning (Graham 2003, Heyman et al. 2005). When not feeding on snapper spawn, whale sharks will feed on a range of alternative foods in shallow (<50 m) and deep (>2000 m) waters including thimble jellyfish (*Linuche unguiculata*), copepods, salps and ctenophores of undetermined species, and further offshore with large schools of little tunny, blackfin and skipjack tuna (Graham 2003). An increase in secondary productivity in late spring linked to the Yucatan upwelling event (Merino 1997) leads to a rise in whale shark abundances between June and September on Mexico's shallow northeast Yucatan shelf Mexico. The majority of encounters are recorded between Holbox and Isla Mujeres (3) (F. Remolina, pers. comm., Yumbalam, Holbox, Q. Roo, 2005). Environmental factors underpinning whale shark visitation in Cuba are as yet unknown, however whale sharks are seen predictably in the remote and relatively unimpacted Jardines de la Reina Archipelago (4), between October and December feeding on pelagic sprat and traveling with schools of little tunny. The archipelago presents a short fore-reef shelf abutting deeper waters north of the Cayman Trench.

Conservation status of whale sharks in the Western Caribbean

Whale sharks benefit from a range of management and conservation measures that enhances their visibility at local, national and international scales. Globally the whale shark is included on the World Conservation Union's Red List of Threatened Species as "Vulnerable" under descriptors VU A1bd+2d (IUCN 2006). Although IUCN listings do not ensure the conservation of a species, they help to increase awareness of their vulnerability with policy-makers. The only international convention or listing that currently confers some form of regulatory measure or protection to whale sharks is the Convention on the International

WHALE SHARKS OF NORTHWESTERN CARIBBEAN



Figure 1. Whale shark feeding aggregation locations ($n = 4$) in relation to marine protected areas and coastal development (orange and red) in the Western Caribbean (Source map courtesy of ReefBase/World Resources Institute 2007).



Figure 2. Whale shark feeding aggregation locations ($n = 4$) in relation to marine protected areas and watershed sources of pollution and sediment (orange and red) in the Western Caribbean (Source map courtesy of ReefBase/World Resources Institute 2007).

Trade in Endangered Species of Fauna and Flora (CITES). In 2002, whale sharks comprised one of 3 shark species to be listed under Appendix II, which provides the framework to monitor and regulate international trade in the species' products. Each of the Western Caribbean countries where whale sharks are currently known to aggregate is party to CITES. Although whale sharks are listed in Appendix II of the convention for Migratory Species (CMS) and on Annex I (Highly Migratory Species) of the UN Convention on the Law of the Sea (UNCLOS), none of the region's countries are signatories to the CMS and Belize, Cuba and Guatemala have not ratified the UNCLOS. National regulations are providing the strongest form of protection for whale sharks with total ban on fishing in Honduras in 1999, Belize (GoB 2000, 2003) and most recently in Mexico (NOM-029-PESC-2006). No laws exist that specifically protect whale sharks in Guatemala or Cuba.

The Western Caribbean possesses a large network of marine protected areas of different designations ($n \geq 32$)⁴, yet satellite and acoustic tagging results suggest that most whale sharks spend little if any time within the boundaries of such protected areas (Graham et al. 2007) as most of these are small, coastal and/or narrowly reef-associated. Belize's Gladden Spit and Silk Cayes Marine Reserve provides protection that encompasses the key whale shark feeding area. This supports the need for knowledge of the location, timing and relative importance of feeding sites to focus whale shark conservation efforts. Gladden Spit was declared a protected area in 2000 after the spatial extent of the aggregation was characterized. Currently, whale sharks congregating in Mexico feed primarily in the unprotected waters between the Isla Contoy and Holbox Protected Areas. Legislation is pending to extend and convert Mexico's Holbox and Contoy MPAs into a broad Biosphere Reserve sanctioned by the United Nation's Educational, Scientific and Cultural Organisation (UNESCO) Man and the Biosphere Programme that would encompass the key whale shark feeding area. In Cuba and Honduras, whale sharks frequently feed and travel outside of the current and proposed protected areas boundaries. However, Honduras is also currently awaiting Government approval for the legal establishment and zoning of the Bay Islands Marine Protected Area that would partially encompass the whale shark feeding site off the northeast coast of Utila.

Media can play an important role in the promoting the conservation of whale sharks. Until 1999, whale sharks benefited from little interest, protection, or management initiatives in the Western Caribbean due to lack of knowledge about the species and its economic importance.

Following widely disseminated results from the Belize whale shark research from 1999 onwards, development of the whale shark tour guide training program and the profile-raising National Geographic Explorer documentary entitled "*Feast of the Giant Sharks*" aired in August 2001, policy-makers bestowed higher priority for conservation planning and research conducted at local, national and regional levels. Project results from efforts highlighted in the documentary further provided the basis for the passing of Statutory Instrument 56 of 2003 that protects whale sharks (GoB 2003).

Threats to whale sharks

Whale sharks face few threats in the Western Caribbean as they are not currently targeted by fisheries. The only known targeted fishery known to have existed in the region was located in Santa Cruz, Cuba, with a take of 8–9 animals a year; however, the fishery was banned by the Cuban Government in 1991 (F. Pina, pers. comm., Centro de Investigaciones de Ecosistemas Costeros, Cayo Coco, Cuba, 2000). Anecdotal reports exist of captures made in Honduras in protest of marginalization of fishers by tourism. These incidents have not been repeated or fully substantiated (D. Afzal, pers. comm., Coral Caye Conservation, Utila, Honduras, 2003). However, the possibility of high-seas capture outside country Exclusive Economic Zones by tuna-purse seiners exists and has occurred in the Indian Ocean (Graham 2003). Instead, threats to whale sharks stem primarily from unregulated tourism, aquaria collections and boat collisions. Research on whale shark behavior indicates that patterns of movement exist, most notably following the bathymetric contours of the Mesoamerican Barrier Reef (Graham 2003, Graham et al. 2007). This north-south path coincides with an important shipping lane that links the United States with the Mesoamerican reef countries. The volume of shipping and more recently cruise boat traffic and its potential impact to the regional whale shark population is undetermined. Coastal Development, cruise ship tourism, rising oil and gas exploration and land-based sources of pollution may pose additional yet site-variable direct and indirect threats to the region's whale shark population (see Figures 1 and 2). According to Burke and Maidens (2004) and Burke and Sugg (2006)⁵ only Jardines de la Reina presents low impact from coastal development, watershed based pollution, and sedimentation with all other sites

impacted variably by a high level of watershed-based sediment and pollution (Gladden Spit and Utila) or coastal development (Cancún-Contoy-Holbox). Burke and Sugg (2006) further suggest that Honduras is responsible for 80% of the sediment load and 50% of pollutants reaching the Mesoamerican Barrier Reef. This material contains a substantial load of organochlorines and organophosphates from agricultural tracts that could affect the reproduction and survival of reef-associated fauna (McField, pers. comm., WWF/Smithsonian Institution, 4 mls Western Hwy, Belize City, Belize, 2005). Finally, global climate change and ocean acidification may further impact whale shark abundance, distribution and patterns of movement following changes in the patterns of primary productivity and hence the availability of predictable food.

Whale shark research characteristics

The number of research projects focused at elucidating the biology and behavior of whale sharks has increased rapidly worldwide in the past 5 years. The first systematically documented observations began in the 1980s noting the seasonal arrival and numbers of whale sharks visiting Ningaloo Reef, Western Australia (Taylor 1996). There are currently at least 19 countries worldwide hosting bona fide whale shark conservation or research projects⁶.

Research began in the Western Caribbean region in 1998 at Gladden Spit in Belize and in Utila, Honduras, followed by a multi-institutional initiative in Mexico's Yucatan Peninsula in 2003 and a brief initiative in Cuba's Jardines de la Reina in 2004. Most of the world's research projects are seeking the same scientific information on whale sharks. Current questions focus on developing a better understanding of whale shark abundance and population structure, biology, feeding and movement behavior, ecology, threats to populations, and conservation opportunities. The degree of advancement in answering any of these questions has varied considerably across sites worldwide.

Whale shark research in the Western Caribbean

In Belize, the questions of movement, philopatry, population size, environmental preferences, threats, conservation and tourism were answered during a study conducted between 1998 and 2004 (Heyman et al. 2001, Graham 2003, Graham 2004, Graham et al. 2006, Graham and Roberts 2007, Graham et al. 2007). Mexico's science program is currently broader in scope due to the participation of a large number of government institutions and

non-governmental organizations coupled with the occurrence of a large and dispersed aggregation. The scientific discovery of the whale shark aggregation at Gladden Split, Belize in 1998 catalyzed the implementation of a comprehensive study of the reef fish spawning aggregations by the Nature Conservancy and of the whale sharks by the University of York from 1999 to 2004. The whale shark project funded primarily by the UK Darwin Initiative and the Natural Environment Research Council encompassed a survey of population abundance and structure using photo identification, marker tags, and feeding behavior. Site fidelity and movement patterns were recorded using conventional, acoustic and satellite archival, and position-only tags. Analysis of stable isotope content in whale shark epidermis and feces coupled with a range of prey species provided indications of whale shark feeding preferences. Biological studies were complimented by demographic and socio-economic studies of the tourism, the snapper fishery, and the snapper spawning aggregations that support the whale shark aggregation. This project was complemented by additional research conducted on whale shark movements and site fidelity of Carcharhinid species by the University of York with the Centro de Investigaciones de Ecosistemas Costeros (CIEC) in the Jardines de la Reina Marine Protected Area in Cuba in 2004. These studies have provided the majority of information on whale sharks in the region that have been disseminated to neighboring Cuba and Mexico and internationally from 2000 onwards.

Mexico's Holbox-based whale shark program was implemented collaboratively between the Government Institution Comisión Nacional de Areas Naturales Protegidas (CONANP) and the NGO Yumbalam in 2003. Having seen the rapid growth of whale shark tourism in Belize, Mexico's first concern in 2003 was to develop whale shark encounter guidelines and regulate the incipient whale shark tourism as a precautionary measure. Lessons from Belize provided the basis for development of guidelines and a research strategy. CONANP and Yumbalam compiled information from fisher, guides and their research crew on seasonality and distribution. With funding from the Georgia Aquarium, the US-based Mote Marine Lab provided visual tags and PSAT tags to help assess population size and movements. Additional whale shark research conducted in Mexico includes DNA population analysis, stable isotope analysis and socio economic valuation of the tourism. Mexico's partnership with the Wildlife Conservation Society and other partners in the regional acoustic array whale shark monitoring program is pending funding but likely to take place in 2007. Although none of the findings have been published as of yet, prelimi-

nary indications suggest important pieces of the regional whale shark puzzle will be resolved shortly.

Whale shark research in Honduras is focused mainly on Utila and encounters take place over 2 km offshore, primarily in the northeast quadrant off the island. Until recently, research was primarily implemented by tour operators offering paying trips for visitors wanting to see whale sharks tagged. The Shark Research Institute tagging program began in 1999 with conventional tags and soon thereafter with the deployment of PSAT tags. Although a web-based resightings form existed for whale shark encounter visitors, no published compilations exist from the submitted data. Currently, 2 tour operators and one local NGO are undertaking whale shark research. Deep Blue is promoting the use of the Ecocean photo ID database⁷ as a non-invasive means of identifying animals (Arzoumanian et al. 2005). The Whale Shark Research and Oceanic Center (WRSOC) is continuing conventional tagging efforts and the Bay Islands Conservation Association (BICA) has worked in the community to develop whale shark tourism guidelines and fisher and tour operator based point maps of seasonal distribution and occurrence. There are additional plans for research to characterize whale shark food preferences, environmental factors influencing whale shark seasonality, and tourism demographics and revenue. With the assistance of the Wildlife Conservation Society, BICA and several tour operators are involved in the regional whale shark monitoring acoustic array that began in February 2007.

Research in Cuba is incipient and primarily conducted at the Jardines de la Reina Marine Reserve based on a partnership of researchers from CIEC, the Wildlife Conservation Society (formerly with University of York) and the private company Avalon that holds the concession to run tours and provide accommodation within the protected area. Whale shark photo identification and PSAT tagging efforts began in 2004. Jardines is one of the sites included in the regional whale shark monitoring acoustic array.

SUMMARY OF RESULTS

Whale shark abundance and population structure

Whale Shark size and population structure is one of the first questions that scientists have tackled worldwide and in the Western Caribbean. There are no estimates for whale shark population size due to their highly migratory nature of its open population. However, through a multi-pronged approach looking at movement, site fidelity

and seasonal abundance, scientists are beginning to piece together a more comprehensive overview of the population size and structure. Both conventional tagging and photo identification are being used in the Western Caribbean to assess population size. Although marker tagging simplifies the identification of individuals, it is non-permanent and invasive. As a result, there are increasing moves to use only photo identification of unique spot patterns to differentiate between individuals. Results to date suggest a minimum population of 106 individuals seasonally visiting Belize based on photo-identification (Graham and Roberts 2007) and over 400 individuals estimated to visit the region of Holbox and Isla Contoy on Mexico's Yucatan Peninsula (R. de la Parra, pers. comm. 2006). There are no estimates of the visiting population for Honduras and Cuba. With sufficient individuals to "tag", mark-release-recapture programs can help to produce relatively robust population estimates, as with Meekan et al.'s (2006) estimate of 319–436 animals at Ningaloo Reef using a Jolly-Seber open-population model.

Analysis of population structure has highlighted sexual and ontogenetic segregation in whale sharks. A 5-year study in Belize revealed a small visiting population of predominantly male and immature animals (Graham and Roberts 2007), findings similar to those recorded in Holbox (R. de la Parra, pers. comm., Yumbalam, Q. Roo, Mexico. 2005). Although large individuals of both sexes are sighted (over 9m, a length at which animals of both sexes are known to be mature), the majority of animals are under 8m. Notably, these data further coincide with mean total lengths recorded in Madagascar⁸, the Seychelles⁹, and Australia's Ningaloo Reef (Meekan et al. 2006). Whether females or larger individuals of both sexes prefer to feed far offshore on pelagic prey in association with several species of tuna or they both comprise a smaller percentage of the regional population is not known and may not be elucidated until larger offshore surveys are conducted.

Whale sharks are known livebearers (Joung et al. 1996) but little is known about pupping and reproductive habitats or mating behavior globally. In the Western Caribbean, aggregations appear to focus on feeding—thus

highlighting critical feeding habitats. Despite the sex ratio bias in favor of immature animals, these sites may facilitate reproduction by bringing together adult whale sharks of both genders, whereby the adults observed are those that move closer inshore to reproduce. Sightings of males in a state of reproductive readiness or having recently finished reproducing (fully extended and calcified claspers that are occasionally observed swollen and frayed) at Belize's Gladden Spit (Graham and Roberts 2007) and in Holbox (R. de la Parra, pers. comm., Yumbalam, Holbox, Q. Roo, Mexico, 2006) strongly suggest that reproduction is taking place in the Western Caribbean. Pupping grounds have not yet been identified as individuals ≤ 3 m are rarely seen with any confirmed sightings or captures of neonates (55 cm to ~ 1 m) in the region.

Site Fidelity

Elucidating whale shark site fidelity underpins research, tourism and conservation success and effectiveness. Marker and acoustic tags coupled with photo identification in Belize have helped to document strong intra- and inter-seasonal philopatry and timing of visitation with onset of snapper spawning events at Gladden Spit (Graham 2003). Similar accounts of philopatry are documented in Mexico (R. de la Parra, pers. comm., Yumbalam, Holbox, Q. Roo, Mexico, 2006) and Honduras (S. Fox, pers. comm., Deep Blue, Utila, Honduras, 2006) as well as other sites including Ningaloo Reef, Australia (Meekan et al. 2006). These results indicate that the identified feeding sites are important to the regional whale shark population and require careful management to minimize impacts to individual and population fitness.

Fine and large scale movements

Although whale sharks display varying degrees of philopatry to at least 3 of the 4 feeding sites identified in the Western Caribbean, whale sharks are highly migratory. Movements take place from one feeding site to another to capitalize on ephemeral yet dense patches of prey. Even though whale sharks are capable of consuming a range of prey using several feeding behaviors, they are physically best adapted to feeding on dense patches of prey (Colman 1997). Gladden Spit offers the best example of the whale sharks timing of both horizontal and vertical movements to snapper spawn, a highly localized, calorific and abundant prey source. Using satellite telemetry, acoustic telemetry linked to passive receivers (Vemco, Halifax, Nova Scotia), conventional tagging (FloyTags, Seattle, WA) and photo identification, whale sharks were documented arriving at Gladden Spit from Glover's Reef (57.7km distance) and Hol Chan Marine Reserve (175km) in time for the onset of

the snapper spawning, following the full moons of March through June. Following cessation of snapper spawning, whale sharks moved both north and south of Gladden Spit up to 6.3km/hr (Graham 2003). Whale sharks marker tagged at Gladden Spit have been resighted near Utila, Honduras and north of Cancún, Mexico further confirming a shared regional population. A total of 22 acoustic tags, 5 smart position-only tags and 11 pop-up archival tags (SPOT and PSAT, respectively; Wildlife Computers, Redmond, WA) were deployed on whale sharks at Gladden Spit and 2 SPOTs tags on whale sharks in Jardines de la Reina between 2000 and 2004. Results document northward and southward patterns of movement along the Mesoamerican Barrier Reef and movement across the deep Cayman Trench from Cuba to the Yucatan (Graham 2003, Graham et al. 2007).

Tagging data indicates that whale sharks do not move towards other regional pulses of productivity in a concerted or social manner. Two satellite-tagged sharks and one conventionally-tagged individual moved towards the feeding site in the NE Yucatan following cessation of feeding at Gladden Spit while other acoustically tagged individuals were documented 35km south of Gladden Spit during the same period (Graham 2003).

Vertical movements are also modulated by food availability. Deep diving patterns that include oscillatory diving interspersed with deeper dives (several recorded over 1000 m) were relaxed during the spring snapper spawning periods. This diving behavior further exhibits strong circa-lunar, circadian and ultradian periodicities (Graham et al. 2006). Although Belize is the only documented site worldwide where whale sharks feed on the spawn of large aggregations of reproducing teleosts, it is highly likely that this natural phenomenon occurs elsewhere. Analysis of the food sources of a recently encountered large aggregation of whale sharks in the northern GOM suggests that the animals were feeding on fish eggs (Hoffmayer et al. 2007, this volume) and anecdotal fisher reports large aggregations of whale sharks associated with large spawning schools of king mackerel (*Scomberomorus cavalla*) off the coast of Isla Mujeres in Mexico (G. Guerrero, pers. comm., Searious Diving, Isla Mujeres, 2005). Further acoustic-tagging studies coupled with regional arrays will likely reveal long-term patterns of site fidelity and movements between feeding sites in the northern GOM and the Western Caribbean. As such, whale sharks could provide the means of identifying additional productive sites, species and natural processes such as spawning aggregations in need of protection, if we could deploy additional satellite tags.

Whale shark tourism

Recognition that whale sharks represent a lucrative tourism attraction has grown steadily over the past decade, both globally and in the Western Caribbean. The region has seen a rapid increase in the number of visitors to all sites except Cuba. Tourists based in the US or transiting from Europe can readily access whale shark sites in Mexico, Belize and Honduras within 2 1/2 hr of flying from several major US gateways. Americans form the bulk of tourist arrivals on the Mesoamerican Barrier Reef whereas Jardines de la Reina's remote location (5 hr from shore) has a maximum capacity of 24 visitors, most of whom are Europeans. A tourism study conducted in Belize in 2002 recorded local visitor expenditures incurred during trips made to encounter whale sharks at Gladden Spit. To derive a rapid estimate of tourism revenue per whale shark, visitor expenditures were divided by the photographically identified population of whale sharks ($n = 106$). Tourism revenue in the whale shark and Gladden Spit's 5 stakeholder communities for the 6-week season in 2002 was estimated at US\$1.35 million and US\$35,000 per shark per year (Graham 2003, 2004). Extrapolated out to the suggested minimum whale shark life-span of 60 yrs, this represents over US\$2 million per shark at Gladden Spit or a minimum of US\$6 million if the whale shark visits all 3 aggregation sites on the Mesoamerican Barrier Reef each year and if revenue is similar at all 3 sites. These calculations are conservative, particularly as tourism revenue is expected to be higher in Cancún or Holbox, Mexico, which receive higher visitation rates yearly than Belize's Placencia. No other contingent valuation methods such as existence value or willingness to pay methods were used in this calculation. By comparison, Davis (Davis 1998b) estimated tourism revenues at Aus\$4.7 (US\$3.1 million) at Ningaloo Reef, Western Australia over a 2-mo season in 1996. This has increased to an estimated US\$10 million value ascribed to the 2.5 month season in 2004 (R. Mau, pers. comm., CALM, Exmouth, Australia, 2005). Newman et al. (2002) estimated potential whale shark tourism revenue of US\$3.95–4.99 million over a 14 week period annually for the Seychelles. With at least 19 sites worldwide that boast of hosting predictable aggregations of whale sharks, encounter tourism could be worth conservatively over US\$42 million annually¹⁰.

The rise in visitation rates at the Mesoamerican whale shark feeding sites has led to iterative efforts in Belize, Honduras and Mexico to manage tourism and mitigate impacts on visiting whale sharks. Belize has transformed the Gladden Spit Marine Protected Area from a marine reserve

with open access, voluntary guidelines and no enforcement in 2000 to a seasonally, heavily enforced, highly restricted and regulated site by 2005. The change was necessary in light of the increase in the number of tour operators from 2 in 1997 to 18 in 2002 to 30 in 2005. The author worked with local community members in 1999 to establish precautionary guidelines for whale shark tourism and developed a whale shark tourism course in response to increased visitor pressure on the temporally and geographically restricted phenomenon of whale sharks feeding on snapper spawn. The NGO Friends of Nature (FON) subsequently capped the number of boats, visitors and amount of time at the site following their establishment as the marine reserve's fully functional management entity in 2001. Tour operators adopted a time slot and lottery system similar to that devised in the mid-1990s for boat access to the highly frequented Shark Reef at Ras Muhammed Marine Park in the Sinai Peninsula, Egypt (R. Graham, pers. observ., Ras Mohammed, 1994). These precautionary actions may not be sufficient: mean encounters with whale sharks have declined from 4 to 6 individuals/d between 1998 to 2001 to < 2/d in 2003 (Graham and Roberts 2007). Anecdotal reports from guides suggest that encounters have remained low since 2003 and further suggest that visitor pressure may still be too high. It appears that divers and boats may disturb whale sharks and reproducing snappers, thus FON and the stakeholder communities have iteratively adjusted the numbers of boats and visitors allowed inside the whale shark zone, and the time slot length. The boundaries of the marine reserve's exclusive whale shark zone have also been modified to track the aggregation's seasonal spatial variation because whale sharks are now under increasing visitor pressure at 3 of 4 feedings sites identified in the Western Caribbean.

The aggregation in Mexico is considered very large (> 400 animals) yet highly dispersed over hundreds of square kilometers (R. de la Parra, pers. comm., Yumbalam, Holbox, Q. Roo, Mexico, 2006). Whale shark tourism has developed primarily from the coastal community of Holbox, where Yumbalam and the Mexican Government has conducted successful guide training and expended considerable efforts on outreach and research to mitigate impacts to whale sharks. However, animals are easily encountered by boat away from Cancún, the busiest tourist hub in the region. With over 2.33 million tourist arrivals recorded in 2004¹¹ and a yearly increase in the number of whale shark tour operators and guides, there is currently no legislation limiting the number of tour operators, guides, visitors or boats that can encounter the whale sharks. Local guides are already noting sporadic incidences of avoidance

behavior where none was ever noted previously. Honduras is currently in the process of developing and legislating tourism and encounter guidelines in the hopes of minimizing tourism's impact on whale sharks and the associated schools of little tunny that local fishers depend on for subsistence and income. The long-term impacts of continuous disturbance by people and boats at feeding sites identified as critical through migratory and site fidelity studies is unknown but could impact the fitness and potential survival of whale sharks in the Western Caribbean.

FUTURE DIRECTIONS

The highly migratory nature of a shared population of whale sharks in the Western Caribbean has made regional accords and collaborative measures imperative. At the broadest scale, promoting the ratification of the CMS would provide an overarching framework for the conservation of the highly migratory whale shark in relation to the undefined threats of shipping and possibly even oil exploration – both of which need to be more fully investigated. Collaboration between countries will further enable sites with fewer resources and results to reach the same level of knowledge about their aggregations as those with longer-term comprehensive studies. The 4 aggregation sites are remarkably different in nature and necessitate different management and conservation strategies. Each can establish site-specific strategies that overlay fundamental guidelines of “not harming whale sharks.” These would include no touching or chasing the animals, establishing a minimum encounter and boat distance from the animal, set times for encounters, and a maximum number of people in the water during an encounter with an individual shark. Standardizing research methodologies related to size estimations, calculating abundances in relation to sampling effort or tourism visitation levels, and sampling of environmental parameters will enable inter-site comparisons globally. Disseminating these results through web sites or even a regional web site linking all research and monitoring efforts as proposed by Reyes (pers. comm. Sept 2006. Regional whale shark tourism workshop) could provide the basis for strategic planning and information exchange during annual regional meetings, e.g., Mexico (2005-2006, 2007) and Belize (2006).

Migratory pathways are only beginning to be revealed through the use of satellite and acoustic telemetry. The development and deployment of a robust and easily deployed fin-mounted SPOT or PSAT tags could provide far greater information on movements over several years. Results need to be analyzed and mapped on a regional scale in the context of bio-oceanographic factors (bathymetry, concentrations of Chlorophyll-a, sea-surface tempera-

ture, dissolved oxygen levels, salinity, current direction and strength, associated species and prey assemblages) and associated shifts in these factors wrought by global climate change. The use of acoustic tags and strategically placed multi-site acoustic array throughout the Western Caribbean and the GOM would complement the satellite technology and help to understand the patterns of site fidelity and timing of movements between multiple feeding sites. This highly robust yet cost-effective technique has been used to great effect in Belize to monitor several large marine species (Graham 2003, Chapman et al. 2005). The array is now set up in Honduras, Belize and selected sites in the GOM. Cuba and Mexico are expected to join the array by mid 2007. Plans have been recently implemented to use the same array to monitor reef-associated Carcharhinid sharks, hawksbill turtles (*Eretmochelys imbricata*) and reef-fish spawning aggregations and will help to test whether whale sharks could act as proxies for other species of ocean giants that are notoriously more difficult to study, e.g., billfish and other large pelagic sharks.

Tourism is the key driving force between most whale shark encounters and research today and assessing its importance is paramount to ensuring its viability. Standardized methodologies that determine visitation scope and scale, economic and existence values, direct and indirect anthropogenic impacts on whale sharks, distribution of benefits and potential growth among others will be key to planning strategies for the sustainability of whale sharks and the associated tourism.

Although wildlife tourism can be lucrative, it can also impact or destroy its target species. One of the key questions posed by conservationists and managers currently is the impact of visitation on whale sharks. In Mexico, Cuba and Honduras where whale shark encounters are undertaken while snorkeling, there is a possibility of assessing and even quantifying whale shark behavior including evasive reactions to visitors and boats. Due to the greater number of variables presented by diving and the reproducing snappers, such assessments will be difficult if not impossible to quantify in a robust manner. As a precautionary measure that would further help to standardize tourism impact on whale sharks, it may be best to ban SCUBA diving on whale sharks at Gladden Spit's spawning aggregation grounds and promote only snorkeling.

A regional assessment of the population size and structure is required to determine the impact of mortality posed by identified threats. Identification of pupping grounds and location of sub-3m juveniles and most females would elucidate sexual and ontogenetic segregation and help to shape more effective conservation measures. Photo identification currently presents the best method available

of assessing population size as the technique is non-invasive, the sharks' spot patterns are permanent, and new computer algorithms enable automated pattern matching (Arzoumanian et al. 2005, Meekan et al. 2006, Graham and Roberts 2007). Although photo identification data collection mechanisms and analysis programs exist, there is need for a system combined with a data-sharing agreement that may be used by all countries to assess both population size and degree of transfer of individuals between sites.

Advances on the multiple fronts described above will enable whale shark stakeholders to piece together a comprehensive long-term picture of whale shark behavioral ecology in relation to protective measures and anthropogenic impacts. This knowledge will provide the basis for increasing the effectiveness of science-based management to sustain visitation of whale sharks at critical feeding sites in the Western Caribbean and elsewhere.

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Where Do We Go From Here? A Summary of Issues of Concern and Recommendations Developed During the Panel Discussion of the Large Pelagic Fishes Symposium

Nancy J. Brown-Peterson

University of Southern Mississippi, nancy.brown-peterson@usm.edu

James S. Franks

University of Southern Mississippi, jim.franks@usm.edu

Mark S. Peterson

University of Southern Mississippi, mark.peterson@usm.edu

Patrick McConney

University of the West Indies, Barbados

Brian E. Luckhurst

Department of Environmental Protection, Bermuda

DOI: 10.18785/gcr.1902.19

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WHERE DO WE GO FROM HERE?

A SUMMARY OF ISSUES OF CONCERN AND RECOMMENDATIONS DEVELOPED DURING THE PANEL DISCUSSION OF THE LARGE PELAGIC FISHES SYMPOSIUM

Nancy J. Brown-Peterson¹, James S. Franks², Mark S. Peterson¹, Patrick McConney³, and Brian E. Luckhurst⁴

¹*Department of Coastal Sciences and* ²*Center for Fisheries Research and Development, The University of Southern Mississippi, 703 East Beach Dr., Ocean Springs, MS 39564 USA, E-mail nancy.brown-peterson@usm.edu*

³*CERMES, University of the West Indies Cave Hill Campus, Barbados*

⁴*Marine Resources Division, Department of Environmental Protection, P.O. Box CR 52, Crawl CRBX, Bermuda*

One of the goals of the Large Pelagic Fishes Symposium was to provide a forum for development of a list of Issues of Concern regarding large pelagic fishes and their fisheries in the Caribbean and Gulf of Mexico region. During the Symposium and ensuing Panel Discussion, it became clear that the level of consciousness concerning large pelagic fishes is of equal importance to that of other regional fisheries such as reef fishes and conch/lobster. Four major issues of concern regarding large pelagic fishes in the region surfaced during the Symposium. The Symposium Committee recommends that future resources and energy should be addressed to these identified concerns:

- 1) Fisheries policy-advisors and managers are not getting information from scientists in a timely fashion;
- 2) Approaches to reduce overfishing and its negative effects need to be strengthened;
- 3) Insufficient attention is being paid to instituting effective regional management; and
- 4) Initiatives to engage fishers in management processes and to help find solutions are inadequate.

Panel members and Symposium participants made a number of recommendations for addressing each of these issues. The recommendations related to helping resolve each issue of concern are listed below.

1. Fisheries policy-advisors and managers are not getting information from scientists in a timely fashion

Abstract 3–4 scientific papers on key subjects each year into a 1 page summary emphasizing the management/policy scenario, and send these to managers to better inform them about cutting edge and critical issues or advances in science.^a

Identify the structure of political systems, as they vary by country; recommendations need to reach the appropriate personnel in each country.^b

Present scientific information to advocacy groups; encourage those groups to talk with managers to explore scientific/political relationships and needs.^{a,b}

Maintain a coherent, long-term direction and include education and advocacy to get the message to appropriate users and stakeholders.^b

Research results need to be better translated from science to assist management.

Decision makers need to be better informed on the issues through workshops and hands-on experiences.^b

2. Approaches to reduce overfishing and its negative effects need to be strengthened

Experts must speak with a clear, consistent voice to avoid confusion regarding scientific recommendations.^a

Managers should make science-based decisions on resource management whenever possible; an attempt should be made to avoid political influence in this process.^b

Scientists must communicate among themselves to avoid presenting conflicting information to managers and fishers.^a

Managers should go into the field to see first hand the impacts of their decisions.

When there is a fisheries collapse/closure, there must be economic solutions that are politically, culturally and socially acceptable for small-scale fishers.^b

3. Insufficient attention is being paid to instituting effective regional management

Create the political will through “grass roots” support and fishers organizations to support regional management initiatives.

Use the success of the CARICOM framework as a model for additional regional management.

Deal more effectively with sovereignty/transboundary issues.

Management should be formulated in the light of political and economic realities.

Use a network analysis approach to provide new perspectives on problems and capacity-building so as to promote integrated management where appropriate.^b

Politicians must support CARICOM/FAO Code of Conduct for Responsible Fisheries and make decisions based on this Code.

Small-scale fisheries must be considered regionally and internationally when designing management plans.

NGO's can be advocates in controversial situations, thus preserving the impartiality of scientists.^b

Identify/develop key relationships and sources of support.^a

Better integration of research efforts is needed to achieve regional goals.

Promote additional and continued partnering between developing and developed countries.

Assess critical gaps in management, including data collection systems.^a

Small and large countries must have equal input into the establishment of rules that affect the region.

4. Initiatives to engage fishers in management processes and to help find solutions are inadequate

Scientists and managers should hire fishers as consultants for their expertise on existing fisheries conditions.^a

Establish scientist/fishers partnerships to increase communications and share knowledge bases by working together.^{a,b}

Scientists should collaborate with existing fishers organizations.

Managers should go sea with fishers to better understand problems first hand.

Encourage fishers, as the ultimate stakeholders, to approach politicians in conjunction with scientists with problems as well as solutions for specific issues.^b

^aAreas in which established regional scientific organizations, such as GCFI and local chapters of the American Fisheries Society, can take a leading role to help address and/or implement a number of these recommendations are indicated in the lists above. The role of the scientific organizations would be to spearhead committee formation or dialogue that would significantly impact these concerns.

^bAreas in which regional, national and international NGOs, such as Environmental Defense, The Nature Conservancy, and the Billfish Foundation can have an important role in helping to address some of these recommendations are indicated in the lists above. These organizations are often uniquely positioned to address situations that cross scientific and political boundaries.

We hope these recommendations, which stem from a broad set of stakeholders throughout the Caribbean Sea and Gulf of Mexico, will initiate and facilitate productive discussions that will allow for enhanced success in forging a more transparent bond between policy, management, and resource sustainability such that cultural, ecological, and economic realities may flourish.

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FISHERIES ECOLOGY ABSTRACTS

TOWARDS AN UNDERSTANDING OF DOLPHINFISH ABUNDANCE: AN INTERPRETATION OF THE RELATIONSHIPS BETWEEN ENVIRONMENTAL VARIABLES AND SPECIES ASSOCIATIONS FROM THE U.S. PELAGIC LONGLINE FLEET

Kirstin Kleisner¹, A.J. Mariano², D. Olson², and Joshua Sladek Nowlis³

¹*Division of Marine Biology and Fisheries, University of Miami, 4600 Rickenbacker Causeway, Miami, Florida 33149 USA, E-mail kkleisner@rsmas.miami.edu*

²*Division of Meteorology and Physical Oceanography, University of Miami, 4600 Rickenbacker Causeway, Miami, Florida 33149 USA*

³*NOAA, Southeast Fishery Science Center, 75 Virginia Beach Dr., Miami, Florida 33149 USA*

Understanding the fluctuations in marine fish stocks is important for the management of fisheries, and attempts were made to demonstrate links with oceanographic and climatic variability. The pelagic longline observer program is a useful tool for studying correlations between environmental and vessel parameters and the various species caught by the longline fleet because of its high spatial resolution, which allows a linkage between the catch data and environmental parameters. We modeled catch-per-unit-effort (CPUE) of dolphinfish (*Coryphaena hippurus*) with several other species that are frequently caught by the United States Pelagic longline fleet in a Principle Components Analysis (PCA) in two distinct biogeographic areas: the Gulf of Mexico and the east coast of the United States. The catch PCA demonstrated that the species were not strongly intercorrelated and therefore dolphinfish were analyzed individually with the environmental parameters. PCAs are presented for dolphinfish individually against oceanic conditions and effort characteristics both for the total datasets and by season for the east and west. In all cases, over 70% of the variability in the data was explained by the first three components. Results suggest that dolphinfish are positively correlated with SST and negatively correlated with proximity of a front, and that the PCAs provide a picture of the areas in each region that are important for higher CPUEs of dolphinfish.

DISTRIBUTION AND ABUNDANCE OF LARVAL TUNAS (SCOMBRIDAE) ASSOCIATED WITH THE LOOP CURRENT, PELAGIC SARGASSUM, AND OCEANIC FRONTAL ZONES IN THE GULF OF MEXICO

Eric R. Hoffmayer¹, Bruce H. Comyns², James S. Franks¹, J. Read Hendon^{1,2}, Richard S. Waller¹, E. Mae Blake¹, and John P. Shelley²

¹*Center for Fisheries Research and Development, Department of Coastal Sciences, Gulf Coast Research Laboratory, The University of Southern Mississippi, PO Box 7000, Ocean Springs Mississippi 39564 USA, E-mail eric.hoffmayer@usm.edu*

Information is lacking on the distribution and abundance of tuna larvae in relation to their seasonal occurrence at oceanic pelagic habitats in the northern Gulf of Mexico. Atlantic bluefin (*Thunnus thynnus*), yellowfin (*Thunnus albacares*), blackfin (*Thunnus atlanticus*), and unidentified tuna larvae (*Thunnus* spp.) were collected during a 2000–2003 investigation of larval and juvenile fishes associated with pelagic *Sargassum* and oceanic frontal zones in the northern Gulf of Mexico, as well as with the Loop Current. Tuna larvae ($n = 380$) occurred in 49% ($n = 77$) of the collections taken during the study ($n = 158$). Larvae were collected from surface and subsurface waters by neuston net (505 μ m), bongo net (333 μ m), and Tucker trawl (333 μ m). Sampling occurred only during day time, and tuna larvae were not collected shoreward of the 300m isobath. Mean abundance of bluefin larvae (3.4 – 8.6 mm; $n = 124$) was highest in collections from the Loop Current boundary and were collected only in May, providing further documentation of a compressed spring spawning season for this species in the Gulf of Mexico. Larvae of yellowfin (3.7 – 7.9 mm; $n = 18$) and blackfin tuna (3.6 – 7.3 mm; $n = 47$) were present in northern Gulf collections at *Sargassum* and frontal zones (none from the Loop Current) from May through August of all years, indicating a protracted spawning season in the region for these species. No tuna larvae were collected in fall and winter. Unidentified larvae (*Thunnus* spp.) require further examination for purposes of species identification. Continued research is critical to advance the scientific understanding of the biology, ecology, and habitat requirements of young tunas in the northern Gulf of Mexico.

ADVANCES IN THE STUDY OF BILLFISH EARLY LIFE HISTORY

Robert K. Cowen

*Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, Florida
33149 USA, E-mail rcowen@rsmas.miami.edu*

Recruitment dynamics of marine fishes are largely driven by processes operating during the early life history (ELH) stages. Yet, for billfishes, the early stages have been only cursorily studied, in part due to the large spatial extent of potential larval and juvenile habitat, difficulties in collecting sufficient numbers of young, and adequately resolving the taxonomic identity of specimens. Early work solved some of the identification issues based on morphological characters, at least for the Pacific, but sufficient resolution was still hampered. Nonetheless, opportunistic sampling, and some targeted efforts, have helped identify potential areas where spawning may be occurring, and provided some idea of the temporal pattern of spawning activity. With the onset of more definitive molecular identification techniques, and advanced sampling systems, more extensive studies into the dynamics of the ELH of billfish are now possible. Here I discuss one such program that was developed to address several aspects of the ELH of billfish within the Western Central Atlantic, with a focus on the Straits of Florida (SOF). Specifically, this study is directed at providing a seasonally-resolved understanding of billfish spawning, larval growth, feeding, and transport within the oceanographic context of the SOF. The work includes measures of the temporal qualities of cross-strait features (i.e., water mass distribution, larval billfish patches, and zooplankton community structure) via monthly sampling (ichthyoplankton, zooplankton, CTD, fluorometry, and ADCP measurements) linked, via otolith aging studies and circulation patterns, to estimates of spawning locations. Otolith work on larval growth rates will be coupled to zooplankton work on community composition and dynamics to identify trophodynamic differences among patches. Ultimately, information on the flux of larvae through this system combined with knowledge of the reproductive output of billfish, may provide estimates of spawning production, and hence, stock size within this region.

DENSITY AND BIOMASS VARIATION OF MICRONEKTON CLOSE TO FISH AGGREGATING DEVICES (FADS) AROUND MARTINIQUE

Laetitia Nelson, Lionel Reynal, and J. Chanterel

Ifremer, Pointe Fort, 97231 Le Robert, Martinique (FWI), E-mail lnelson@ifremer.fr

The numerical and ponderal variations of micronekton around fish aggregating devices (FADs) have been studied in Martinique using day/night sampling from upper 200 m depth with a mesopelagic trawl. The trawl used is an Isaac Kidd-like type, of 7,13 m² surface to the opening and a grid of four mm at the bottom. Forty six samples have been collected between July 2003 and April 2004. A total of 189 taxons of fish, squids and crustaceans covering 86 families were collected. In this article the micronekton's density and biomass variations are described using four parameters: the season, the day/night comparison, the depth and the distance to shoreline. The most abundant taxa composition in the samples is described in order to understand what participation they have in the diet of tuna.

FISH AND INVERTEBRATE IDENTIFIED DURING THE LESSER ANTILLES PELAGIC ECOSYSTEM PROJECT (LAPE), 26 APRIL TO 9 MAY 2006

L. Nelson¹, L. Reynal¹, J. Rambally², S. Punnett³, H. Oxenford⁴, and P. Fanning⁵

¹Ifremer, Pointe Fort, 97231 Le Robert, Martinique (FWI), E-mail lnelson@ifremer.fr

²Department of Fisheries, St. Lucia

³Ministry of Agriculture Forestry and Fisheries, Richmond Hill, Kingstown, St. Vincent

⁴Centre for Resource Management and Environmental Studies (CERMES), University of the West Indies, Cave Hill Campus, Barbados

⁵Secretary of WECAFC, United Nations House, Marine Gardens, Christ Church, PO Box 631-C, Bridgetown, Barbados

During the LAPE ecosystem survey, forage fish distribution and abundance have been estimated by acoustics. At points selected from acoustic traces, net sampling, with pelagic trawl or multi-net nekton sampler, has been used to obtain biological specimens of the acoustic target. The samples captured during the survey are introduced with

pictures and the most important identification criteria used. The described micronekton is essentially composed of fishes, cephalopods, gastropods and crustaceans. This set of sheets is proposed as a reference collection to help in pelagic top predators stomachs contents identification in the Lesser Antilles.

ACOUSTIC BIOMASS ESTIMATES OF PELAGIC FORAGE SPECIES IN THE OFFSHORE WATERS OF THE LESSER ANTILLES

Gary Melvin¹, Paul Fanning², Ciaran O'Donnell³, and Martin Dahl⁴

¹*St. Andrews Biological Station, St. Andrews, New Brunswick, Canada, EOG 2X0, E-mail melving@mar.dfo-mpo.gc.ca*

²*FAO Subregional Office for the Caribbean, PO Box 631-C, Bridgetown, Barbados*

³*Fisheries Science Service, Marine Institute, Rinville, Oranmore, Co. Galway, Ireland*

⁴*Institute of Marine Research, PO Box 1870 Nordness, 5817 Bergen Norway*

A recently completed survey of the Lesser Antilles pelagic ecosystem used a combination of multi-frequency acoustics and pelagic trawling to locate and estimate the biomass of forage species. Stratified zig-zag transects covered the waters east and west of the Lesser Antilles from Antigua to Trinidad. Distinct pelagic layers and aggregations observed acoustically were sampled using a multiple (3) codend pelagic trawl. Pelagic organisms were identified to the lowest taxon possible and categorized by presence or absence of a swim bladder. The acoustic data were grouped into nine broad categories based on the multi-frequency returns considering backscattering strength, aggregation appearance, depth and time of day. The resulting acoustic density was converted to indicative biomass density (kg/m²) by application of target strength estimates from published sources. Relative abundance and composition of the nine acoustically classified groups are presented.

SPATIAL AND DIEL DISTRIBUTION OF PELAGIC FORAGE SPECIES THROUGHOUT THE LESSER ANTILLES FROM AN ACOUSTIC AND MID-WATER TRAWL SURVEY

Paul Fanning¹, Gary Melvin², Ciaran O'Donnell³, and Martin Dahl⁴

¹*FAO Subregional Office for the Caribbean, PO Box 631-C, Bridgetown, Barbados, E-mail paul.fanning@fao.org*

²*St. Andrews Biological Station, St. Andrews, New Brunswick, Canada, EOG 2X0*

³*Fisheries Science Service, Marine Institute, Rinville, Oranmore, Co. Galway, Ireland*

⁴*Institute of Marine Research, PO Box 1870 Nordness, 5817 Bergen Norway*

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COMPOSITION, DIVERSITY, AND RELATIVE ABUNDANCE OF OCEANIC SHARKS IN THE CARIBBEAN SEA AND ADJACENT WATERS

Rafael Tavares^{1,2} and Freddy Arocha²

¹*Centro para la Investigación de Tiburones (CIT), Av. Don Bosco, Qta ABC, La Florida, Caracas 1050, Venezuela, E-mail: rtavares@sucre.udo.edu.ve*

²*Departamento de Biología Pesquera, Instituto Oceanográfico de Venezuela, Universidad de Oriente, Cumaná 6101, Venezuela*

The information analyzed was obtained by scientific observers on board the Venezuelan pelagic longline fleet targeting swordfish and tuna during 1994–2003. The total shark bycatch comprises a total of 25 species, in which the most frequently caught were *P. glauca* (34.76%) and *C. signatus* (20.15%). Other common species in the catch composition were *C. falciformis* (8.46%), *S. mokarran* (6.81%), and *I. oxyrinchus* (6.23%). Shark diversity analysis showed a decreasing trend throughout the time series. Areas with relative high diversity values were located in the southeastern Caribbean Sea, primarily in areas close to the islands and coasts of Venezuela. Other areas with significant diversity values corresponded to the inner arc of the Lesser Antilles and Suriname shelf. Annual CPUE trends for the five most important shark species revealed a declining in abundance during the time series. Shark catches for the most important species comprised a large proportion of juveniles. Major efforts, with support from the international community will be needed to generate the information required for the stock assessment of pelagic and coastal sharks in the Caribbean Sea.

ASPECTS OF THE BIOLOGY OF SHARKS IN THE FISHERY OF THE YUCATAN PLATFORM

David E. De Anda-Fuentes¹ and M.E. Vega-Cendejas²

¹*Centro Regional de Investigación Pesquera de Yucalpetén. AP. No 73, Progreso, Yucatán, México Cp. 97320, E-mail deandadavid@yahoo.com*

²*Centro de Investigación y Estudios Avanzados-IPN. AP. No. 73, Cordemex, Yucatán México. Cp. 97310, E-mail maruvega@mda.cinvestav.mx*

Shark capture in the state of Yucatan has increased from 450 ton in 1975 to 1,300 in 1994, thus occupying 4th place by its economic value and 7th place in importance considering its capture volume at the national level. Although the biological and fishing knowledge of this resource is essential to establish the rules for its management, little is known about the abundance and spatial-temporal distribution pattern of the species. The objective of the present study was to contribute to the knowledge of the population structure of the shark resource in Yucatan platform. The information gathered from 1985 to 1991 comes from ship records (knowledge of fishing area, depth, composition and weight of the capture, meristic data) and fishing landings (biological data). For the analysis of the community structure by zones and depth, a binary matrix of data was built (presence/absence) and multivariate analyses were carried out. The capture is composed of 27 species within 9 families. Dominant species, considering Sanders Index, were *Carcharhinus falciformis*, *Rhizoprionodon terraenovae*, *Mustelus norrisi* and *Sphyrna tiburo* as well as *Hexanchus vitulus*, a species that was not reported before for the area. Five fishing areas were identified, and the east of the state was the one with the most fishing pressure. Most shark species showed a seasonal pattern, being captured most frequently during summer and autumn. In capture terms, the genus *Carcharhinus* supported the shark fishery with almost 50% of the records. Diverse association levels were obtained between species and areas. In relation to administration, the information doesn't allow formulation of regulations. However, already some preliminary recommendations have been considered, with a suggestion to not increase the fishing permissions for shark capture. It is concluded that some shark species in the Yucatan coast have suitable areas for living and breeding, but they have been subjected to heavy fishing efforts that could generate in the near future the collapse of this resource.

BIOLOGICAL STUDIES OF THE WHALE SHARK AGGREGATION OFF ISLA HOLBOX AND ISLA CONTOY, WHERE THE GULF OF MEXICO MEETS THE CARIBBEAN SEA

R. Hueter¹, R. De La Parra², J. Tyminski¹, M. Trigo Mendoza², C. Simpfendorfer¹, J. Gonzalez Cano², F. Remolina Suarez², and J. Perez Ramirez²

¹Center for Shark Research, Mote Marine Laboratory, 1600 Ken Thompson Parkway, Sarasota, Florida 34236 USA, E-mail rhuetter@mote.org

²CONANP-SEMARNAT, Blvd. Kukulcan Km.4.8 Zona Hotelera, C.P. 77500, Cancun, Quintana Roo, Mexico

Between mid-April and September each year, large numbers of whale sharks (*Rhincodon typus*) visit continental shelf waters off Mexico's Isla Holbox and Isla Contoy where the northwestern Caribbean Sea meets the southeastern Gulf of Mexico. Biological studies of these huge, pelagic planktivores to document their distribution, number, size, sex, behavior and migration began off Quintana Roo in August 2003, and have continued through 2006. Research methods comprise a combination of on-water and aerial surveys, tagging and tracking with visual and satellite tags, and logbook data collection by local guides and fishermen. Genetic tissue samples also have been collected for collaborating institutions. All data indicate at least several hundred whale sharks visit the area every summer to feed on plankton associated with a seasonal upwelling. Approximately 400 individual sharks have been tagged primarily in the summers of 2004–2006. Estimated size of observed sharks ranges 2–13 m TL; tagged animals range 3–12 m TL, with an average size of 6.7 m TL. Sex ratio is approximately one female for every 2–3 males. Mature and immature animals of both sexes are present. Resightings of tagged animals have been reported over 300 nm away from the tagging site and in subsequent years back at the site. Pop-off (PAT) satellite-tagging has confirmed migrations of nearly 900 km in one month and dives to at least 980 m when the sharks move off the Campeche Bank. Based on the number of animals documented to date, this area where the Gulf of Mexico meets the Caribbean Sea appears to be one of the world's most important population centers for the whale shark.

MERCURY CONTENT OF LARGE PELAGIC FISHES FROM THE NORTHERN GULF OF MEXICO

Harriet Perry¹, Henry Folmar², Barbara Viskup², Emily Cotton², Tony Lowery³, Kenneth Powell³, Faye Mallette¹, and James Franks¹

¹Center for Fisheries Research and Development, Gulf Coast Research Laboratory, The University of Southern Mississippi, PO Box 7000, Ocean Springs, Mississippi 39566 USA, E-mail harriet.perry@usm.edu

²Mississippi Department of Environmental Quality, PO Box 20305, Jackson, Mississippi 39289-1305 USA

³National Seafood Inspection Laboratory, National Marine Fisheries Service, 3209 Frederic Street, Pascagoula, Mississippi 39567 USA

The waters of the northern Gulf of Mexico (nGOM) support valuable recreational fisheries with many species retained for consumption. Evidence of the link between fish consumption and elevated levels of mercury in human tissue continues to accumulate. An investigation of total mercury levels in large pelagic fishes from the nGOM was initiated in the summer of 2006. Blue marlin (*Makaira nigricans*), yellowfin tuna (*Thunnus albacares*), wahoo (*Acanthocybium solandri*) and dolphin (*Coryphaena hippurus*) were sampled at Mississippi docks during fishing tournaments. Fish tissue sampling protocols and analytical techniques (direct mercury analysis) followed those used in a synoptic survey of total mercury in recreational finfish conducted by the National Seafood Inspection Laboratory, NOAA Office of Sustainable Fisheries. There were significant positive relationships between size and mercury concentrations in yellow and blackfin tunas, wahoo, dolphin, little tunny, and king mackerel. Highest individual value for total mercury was found in blue marlin (9.630 ppm) with an mean ($n = 6$) concentration of 7.099 ppm.

POPULATION STRUCTURE AND MOVEMENTS ABSTRACTS

BLUE TRAVELERS: IS THE SUSTAINABILITY OF ATLANTIC BLUEFIN TUNA AND BLUE MARLIN STOCKS LINKED TO THE GULF OF MEXICO?

Jay Rooker¹, Dave Secor², Richard Kraus¹, and Scott Holt³

¹Texas A&M University, Department of Marine Biology, 5007 Ave U, Galveston, Texas 77551 USA, E-mail rookerj@tamug.edu

²Chesapeake Biological Laboratory, University of Maryland Center for Environmental Science, P.O. Box 38, Solomons, Maryland 20688 USA

³The University of Texas at Austin, Marine Science Institute, 750 Channel View Drive, Port Aransas, Texas 78373-5015 USA

Atlantic bluefin tuna and blue marlin are highly migratory species that commonly cross ocean basins or political boundaries, and thus the fate of each species is influenced by activities (i.e. fishing) throughout their home range. Here, we examine the role of the Gulf of Mexico as essential fish habitat (EFH) of bluefin tuna and blue marlin, and report on the movement and stock structure of individuals that frequent this marginal sea at some part in their life history. Data from several sources support the premise that the Gulf serves as EFH of bluefin tuna and blue marlin, and the region appears critical to the sustainability of both species. Observer data and logbook catch records from the U.S. long-line fleet demonstrate that both species frequent the Gulf and occupy the northern section of this basin during presumed spawning periods. Larval distribution data support the assertion that the Gulf represent critical spawning habitat of both species as well as other large pelagic species, which commonly aggregate along "hot spots" of productivity in the northern region. Electronic tagging and otolith chemistry data further document utilization patterns in the Gulf and highlight the unique nature of bluefin tuna and blue marlin populations. For bluefin tuna, residency times are limited and directed movements out of Gulf occur after spawning in a predictable manner. Long-distance movement often occurs after leaving the Gulf and a similar pattern of movement occurs for the eastern stock (spawns in Mediterranean Sea), which intermingle with Gulf-spawned individuals as they migrate into the western and central Atlantic. In contrast, movements of blue marlin out of the Gulf appear less directed with a large fraction of the population remaining in the Gulf from summer spawning periods into the winter. As a result, the Gulf component of blue marlin may have a separate migration pathway from the Atlantic population. The theory of distinct population components or contingents appears to apply to both Atlantic bluefin tuna and blue marlin in the Gulf, and further information on movement and population structure of both species is clearly needed to effectively manage these pelagic voyagers.

GENETIC VARIABILITY OF THE WHALE SHARK (*RHINCODON TYPUS*) IN TWO ISOLATED POPULATIONS: CARIBBEAN (HOLBOX ISLAND) AND GULF OF CALIFORNIA

Dení Ramírez-Macías¹, Ricardo Vázquez-Juárez¹, Felipe Galván-Magaña², and Rafael De La Parra³

¹Laboratory of Biotechnology of Marine Organisms, Centro de Investigaciones Biológicas del Noroeste, Mar Bermejo 195, Col. Playa Palo de Santa Rita, La Paz, B.C.S. 23090, México, E-mail tiburonballena@gmail.com

²Department of Fisheries, Centro Interdisciplinario de Ciencias Marinas, Av. Instituto Politécnico Nacional s/n Col. Playa Palo de Santa Rita, La Paz, B.C.S. 23096, México

³Proyecto Dominó (Tiburón Ballena del Atlántico Mexicano), Av. Xel-ha 1-311, SM 28, Cancún, Quintana Roo 77500, México.

The whale shark (*Rhincodon typus*) is epipelagic with a circumtropical distribution. The whale shark has a K-selected life history that makes it vulnerable to exploitation, such as large size, slow growth, late maturation, extended longevity, and probably small populations. It is a highly migratory organism, and sustainable use of this threatened species depends on international collaboration. Our knowledge of its biology, ecology, and behavior is limited and hampers our ability to implement appropriate protection for conservation. In 2000 whale shark was listed as vulnerable on the IUCN Red list and was included on the red list in Mexico in 2001 because of the population decline in the last years which could result in a negative effect on their populations. To properly manage the species, it is

necessary to assess levels of inter- and intra population variation so that management units can be accurately defined. Quantification of inter- and intra-specific sequence variations within the mitochondrial (mtDNA) genome is a powerful tool for examining questions of population genetic structure, gene flow, and migratory movements within and among different populations of sharks. In collaboration with the National Commission of Protected Natural Areas (Área de Protección de Flora y Fauna Yum Balam and Parque Nacional Isla Contoy), a project was undertaken to study the population genetics of the whale shark. A highly variable fragment of the mtDNA control region of the whale shark was amplified and sequenced to characterize the amount of genetic variation within populations in the Gulf of California ($n = 65$) and Holbox Island in the Caribbean Ocean ($n = 58$). We found higher levels of variation in the Gulf of California with 23 haplotypes ($h = 0.92$, $\pi = 0.01$) than the Holbox Island with 15 haplotypes ($h = 0.78$, $\pi = 0.01$). AMOVA analysis revealed significant geographic difference among the two ocean basins, indicating that the whale shark populations are structured on a geographic scale.

BEYOND THE SPECIES ID OF THE EARLY STAGES OF TUNAS AND BILLFISH: THE ADVANTAGES OF DNA SEQUENCING

J. R. Alvarado Bremer^{1,2}, J. Bangma², T. Talley-Farnham², J. Rooker^{1,2}, and B. Saxton²

¹Texas A&M University at Galveston, Department of Marine Biology, 5007 Ave U, Galveston, Texas 77551 USA, E-mail alvaradj@tamug.edu

²TAMU, Department of Wildlife and Fisheries Sciences, 210 Nagle Hall, TAMU 2258, College Station, Texas 77843 USA

Early life history stages of tunas and billfish are difficult to identify based on meristic and morphological characters. Advances in molecular genetics techniques based on the polymerase chain reaction (PCR), have over the last decade provided means to identify (ID) fish larvae using minute amounts of tissue preserved in a variety of ways. Here we present data generated to the forensically ID tuna and billfish larvae from the Gulf of Mexico, and tuna larvae from the Gulf of Guinea, based on nucleotide polymorphisms of the mitochondrial DNA (mtDNA) control or d-loop region. While other molecular ID techniques, such as PCR-RFLPs and multiplex PCR assays, are faster and more economical to conduct than sequencing, they do not contain the wealth of information stored in sequence data. We illustrate these added benefits of sequencing with studies of tunas and billfish in the areas of population structure, assessments of historical demography and estimates effective population size, molecular systematics, molecular ecology and evolution, and the assessment of reproductive variance and other behavioral correlates.

STUDIES OF YELLOWFIN TUNA AGGREGATIONS AROUND DEEPWATER PETROLEUM PLATFORMS IN THE NORTHERN GULF OF MEXICO

Randy E. Edwards¹ and Kenneth J. Sulak²

¹University of South Florida, St. Petersburg, USGS-FISC, 600 4th St. S, St. Petersburg, Florida 33701 USA, E-mail redwards@usgs.gov

²USGS Florida Integrated Science Center, Gainesville, 7920 NW 71st St Gainesville, Florida 32653 USA

Oil and gas production in the northern Gulf of Mexico has expanded into deep waters of the outer continental shelf, where the deepwater petroleum structures (DPSs) act as fish aggregating devices (FADs) for tunas and other species. We initially studied yellowfin tuna (YFT) aggregations around a DPS by tracking acoustic-tagged fish from a research vessel (Edwards and Sulak, 2006) and more recently, around a large spar platform, *Medusa*, 69 km off the Mississippi delta moored in 678 m depth, by attaching automatic receivers to the platform at 9 m depth, and tagging 31 YFT with surgically-implanted, coded acoustic transmitter tags in July, 2005. Most fish remained highly associated with the platform, with many present for relatively long, continuous periods without day-scale absences early in the monitoring period; many returning for periods of several days after day-scale absences; some returning more than one time; and several returning after long absences. The pattern of residence was dissimilar to other, disparate patterns reported in comparable studies of YFT at FADs and seamounts, showing that YFT aggregation, residence, movement, and migration patterns are complex and vary greatly from location to location. The patterns observed in this study suggest that DPSs greatly affect YFT presence, distribution, movement, catchability, and possibly population structure in the northern Gulf of Mexico. Because the impact is potentially large, a new study is being planned for 2007, in which all or most of the DPSs in the Mississippi Canyon area will be instrumented, and a large number of YFT (~150) will be tagged and monitored. Additionally, YFT movement to and from a natu-

ral bathymetric feature (Sackett Bank = Midnight Lump), an area of aggregation during winter supporting a large recreational fishery, will be assessed by tagging some fish there and by deploying monitoring instruments during winter 2007–2008.

MOVEMENT PATTERNS AND HABITAT PREFERENCES OF WAHOO, *ACANTHOCYBIUM SOLANDRI*

T. Theisen and J. Baldwin

Division of Biological Sciences, Florida Atlantic University, 2912 College Avenue, Davie, Florida 33314 USA, E-mail ttheisen@fau.edu

The wahoo, *Acanthocybium solandri*, is an offshore marine fish which inhabits tropical, subtropical, and warm temperate waters worldwide. Wahoo are reported to be highly migratory and to visit a wide variety of open ocean habitats, and are economically important over most of their range. Despite this mobility and commercial value, there is very little scientific data concerning the movement patterns or habitat preferences of wahoo. This presentation describes our research project using pop-up satellite tags (PSAT's) to study the movements and habitat preferences of wahoo in the western Atlantic Ocean. A PSAT is a technologically advanced wildlife tag which can monitor the movements of pelagic fishes, independent of potentially biased commercial fishery data. Computer chips on-board each PSAT measure and record water depth, water temperature, and fish position over a pre-determined period of time. At the end of this period, the PSAT's on-board computer initiates a detachment signal and the positively buoyant tag floats to the surface. The stored data is transmitted to a satellite and then to the researcher's computer via electronic mail and the World Wide Web. This presentation describes the protocol used to capture, tag, and release wahoo and presents preliminary data obtained from the first several tags to be successfully deployed.

FROM CAPE COD TO THE GULF OF MEXICO: MOVEMENT AND BEHAVIOR OF OCEAN SUNFISH, *MOLA MOLA*

Inga F. Potter and W.H. Howell

Department of Zoology, University of New Hampshire, Durham, New Hampshire 03824 USA, E-mail inga.potter@unh.edu

During the pilot season of a three-year PSAT tagging project of ocean sunfish, *Mola mola*, in the northwest Atlantic, an ocean sunfish was tagged and released with a pop-up satellite archival tag off of Cape Cod, MA and tracked for 130 days. The fish traveled a distance of approximately 3,000 km to the Gulf of Mexico. Vertical movement of the fish in waters off New England after initial tagging was at depths ≤ 200 m with large amounts of surface time, as was consistent with two other fish tagged in the area. However, as the fish moved southward, its vertical behavior changed to increased time at depth (200–500 m) and no time at the surface. Maximum depth for the fish was 591 meters. The fish spent the majority of time in waters between 10–20°C, experiencing increased temperatures when it entered the Gulf of Mexico. In the project's first field season following the pilot study, 15 fish were tagged with PSAT's in the northwest Atlantic during the months of July and August 2006. The objectives of the study are to: 1) determine the spatial and temporal distribution of *Mola mola* off the northeast coast of the United States; 2) study their movement and migratory patterns; and 3) quantify temperature and depth preferences of *M. mola*. In addition to tagging, the project includes analysis of aerial sightings of *Mola mola* in northeast shelf waters from several databases (1974–present).

MANAGEMENT: STRATEGIES, PROBLEMS AND SOLUTIONS ABSTRACTS

LARGE PELAGIC SPECIES PERMIT HOLDERS IN THE CARIBBEAN SEA AND GULF OF MEXICO: STATISTICS, CHARACTERISTICS, AND DEMO- GRAPHIC TRENDS

Ronald J. Salz and John Foster

*National Oceanic and Atmospheric Administration, National Marine Fisheries Service,
Fisheries Statistics Division F/ST1, 1315 East-West Highway, Silver Spring, Maryland, USA,
E-mail ron.salz@noaa.gov*

Vessel owners who fish recreationally for regulated tunas, sharks, swordfish, and billfish in US federal waters of the Caribbean Sea and the Gulf of Mexico must obtain a Highly Migratory Species (HMS) permit. Vessel owners who fish commercially for regulated tunas in the Caribbean Sea and the Gulf of Mexico must obtain an Atlantic Tunas permit. This paper explores statistical and demographic trends over the past seven years in US vessels permitted to fish for large pelagics in the Caribbean Sea and Gulf of Mexico. Data from permitted vessels with principle ports in the following states/territories were included in this study: Florida, Alabama, Mississippi, Louisiana, Texas, Puerto Rico, and the US Virgin Islands. Historical permit databases were analyzed for the three largest permit categories for large pelagic species: HMS Angling category, HMS Charter/Headboat category, and Atlantic Tunas General category. Trends in the number of permits sold by category, principle port state/territory, and city were investigated. This study also assessed the prevalence of permit category switching over time and evaluated turnover among Caribbean and Gulf of Mexico large pelagics fishing vessels based on persistence in permit databases. Vessel length was also analyzed by permit category and principal port state. Implications of these findings for the management of large pelagic fishes in the Caribbean Sea and Gulf of Mexico are discussed.

SPATIO-TEMPORAL PATTERNS IN THE GULF OF MEXICO PELAGIC LONGLINE FISHERIES

Craig Brown¹ and Karina Ramirez Lopez²

*¹Southeast Fisheries Science Center, NOAA Fisheries, 75 Virginia Beach Drive, Miami, Florida,
33149 USA, E-mail craig.brown@noaa.gov*

*²Instituto Nacional de la Pesca-Veracruz, Av. Ejército Mexicano No. 106, Col. Exhacienda
Ylang Ylang, Boca del Río, Veracruz, Mexico C.P. 9429*

This poster presents data on the spatio-temporal patterns of effort and catches by United States and Mexican pelagic longline fleets operating in the Gulf of Mexico. These data were collected through the scientific observer programs of each country, beginning in 1992 for the U.S. and in 1993 for Mexico. The combined database was jointly analyzed under the auspices of MexUS-Gulf (the cooperative program between the U.S. National Marine Fisheries Service and the Mexican National Fisheries Institute, INP). The distribution of effort across years and seasons/quarters is examined, along with its relationship to depth contours and to other factors such as seas surface temperature patterns. Likewise, the distribution of catches is studied, scaled by relative catch rate levels. The primary focus is on yellowfin tuna (*Thunnus albacares*) as this is the main target species of these fisheries, but attention is also given to various other species which are caught.

RECREATIONAL CATCH AND RELEASE: RESOURCE ALLOCATION BETWEEN COMMERCIAL AND RECREATIONAL FISHERMEN

C. Phillip Goodyear

1214 N Lakeshore Drive, Niceville, Florida 32578 USA, E-mail philgoodyear@cox.net

Recreational catch and release is a management option for some species that are treasured for their sporting value. This management option for shared fisheries is not entirely compatible with the management objective of obtaining maximum sustainable yield as envisioned by many management institutions. Released recreational catch can simply be caught and removed from the population by commercial interests thereby increasing their catches while still maintaining the population at the same level. A logistic surplus production model is applied to an arbitrary fish stock to show that if the commercial harvest is not allowed to increase, the stock will grow because of the recreational releases, eventually resulting in higher catch rates for both recreational and commercial fishers. This option has the potential to benefit both user groups.

FILLING THE INFORMATION GAP: THE BILLFISH FOUNDATION'S COOPERATIVE TAGGING PROGRAM

D. Bogardis, R. Nelson, E. Peel, and P. Chaibongsai

2161 E. Commercial Blvd, 2nd Floor, Ft. Lauderdale, Florida 33308 USA, E-mail ellen_peel@billfish.org

The Billfish Foundation's (TBF) Cooperative Billfish Tagging Program began in 1990 and to date has compiled data on over 130,000 animals. Tag and recapture efforts occur in the Atlantic, Pacific and Indian Oceans. The program is built upon the volunteer support of anglers, captains and mates and provides the means to generate large tagging data sets in a cost effective fashion. This paper reports on recent program advances; including increased international outreach efforts and a web-based data entry and retrieval system.

STOCK ASSESSMENT AND MANAGEMENT ADVICE FOR THE KING MACKEREL (*SCOMBEROMORUS CAVALLA*) FISHERY OF TRINIDAD AND TOBAGO

Daniel D. Hoggarth¹ and Louanna Martin²

¹Scales Consulting Ltd, 66b Creffield Road, London W3 9PS, UK

²Fisheries Division, Ministry of Agriculture, Land and Marine Resources, 35 Cipriani Boulevard, Port of Spain, Trinidad and Tobago, E-mail mfau@tstt.net.tt

This paper reports on a stock assessment of an assumed 'southern Caribbean' stock of king mackerel, based on length frequency data collected in Trinidad and Tobago mainly in the years 1996 to 1998 (total $n = 2200$), and a second smaller data set from 2004 ($n = 558$). Von Bertalanffy growth rates were first estimated using the combined 1996–98 data set in the FMSP LFDA package. The analysis provided two sets of growth parameters, a 'low L_{∞} ' model ($L_{\infty} = 130\text{cm}$, associated with a K of 0.35), and a 'medium L_{∞} ' model ($L_{\infty} = 155\text{cm}$, with a lower K of 0.30), both of which provided equally good fits to the main modes in the data set. Total mortality rates (Z) were estimated for each of the two growth models as 1.26 and 1.70 for the 1996–1998 data set, and as 1.99 and 2.50 for 2004. With estimated natural mortality rates (M) of 0.59 and 0.51 for the low and medium L_{∞} growth models respectively, fishing mortality rates, F , were estimated as 0.67 and 1.19 for 1996–1998 and 1.40 and 1.99 for 2004. An 'analytical' or 'per-recruit' model was then fitted using the FMSP 'Yield' software, using a standard Beverton and Holt formulation. Based on a draft objective of "maintaining the sustainability of resources", the $F_{20\%SPR}$ reference point was adopted as an upper limit or threshold fishing mortality rate, that should not be exceeded. The two growth models gave $F_{20\%SPR}$ estimates of 0.80 and 0.66. The 1996–98 fishing rates were thus either 16% below or 80% above the $F_{20\%SPR}$ reference point, depending on which growth model was used. For the higher 2004 estimates of fishing mortality rates, both models suggest that the fishery was operating well above the assumed 'safe' levels of the $F_{20\%SPR}$ reference point (i.e., 85–202% above). Consideration was given to adjustments in fishing effort levels that could be used to reduce F to below the limit reference points. Guidance was also provided on closed seasons and fish size limits that could alternatively be used to maintain spawning stock biomass per recruit above the limit 20% level. Due to the small length frequency sample size available in 2004 and the high level of uncertainty in

the analysis, the study concluded that new length data should be collected urgently to clarify the current position of the fishery. Responsible management will also require improved understanding of the stock distribution, and the harmonization of management measures in each of the states that share this stock.

REMOTELY SENSED RED TIDE FEATURES AND THEIR RELATIONSHIP WITH RECREATIONAL KING MACKEREL CATCH OFF WEST-CENTRAL FLORIDA

Carrie Wall¹, Frank Muller-Karger¹, M. Roffer², and C. Hu¹

¹College of Marine Science, University of South Florida, 140 7th Ave S, St. Petersburg, Florida, 33701 USA, E-mail cwall@marine.usf.edu

²Roffer's Ocean Fishing Forecasting Service, Inc., 60 Westover Drive, West Melbourne, Florida, 32904

A strong red tide caused by the toxic dinoflagellate *Karenia brevis* was present off of the central West Florida Shelf from January through at least November 2005. A new technique to use solar stimulated phytoplankton fluorescence, from the MODIS Fluorescence Line Height (FLH) data product, was used to remotely sense phytoplankton concentrations in the ocean surface. Algorithms to detect frontal features in satellite-derived FLH, chlorophyll concentration, and turbidity images were used to study the linkages between recreational catch of king mackerel (*Scomberomorus cavalla* or kingfish) and red tides in coastal waters off west-central Florida. The FLH data were used to characterize the spatial distributions of the red tide and its features over the course of 2005. FLH data allowed clear identification of chlorophyll patches as opposed to darker waters related to river discharge along the coast. A Geographical Information System (GIS) tool was used to examine spatial relationships between catch data and ocean fronts, bathymetric features, the presence of baitfish, and the stability of fronts over the three-day period leading up to the tournaments. There was a strong correlation between the presence of baitfish and kingfish catch rates, and catch rates decreased in more turbid waters identified in ocean color imagery. Concurrent with the 2005 red tide event a significant decrease in kingfish catch was found in the fall of 2005 (208 kingfish) compared to spring 2004 (444) and 2005 (538), and fall 2004 (818). Percentages of fishing locations where baitfish were observed also decreased in the fall 2005 (38%) compared to spring 2004 (54%) and 2005 (51%), and fall 2004 (54%). Quantifying the relationships between kingfish catch and its forage is an essential step in forming ecosystem-based management strategies. Satellite data is important in defining ecosystem-scale connections.

DESCRIPTION AND CONSERVATION IMPLICATIONS OF MARTINIQUE FAD FISHERIES

L. Reynal¹, E. Morize², L. Nelson¹, J.J. Rivoalen¹, and A. Lagin¹

¹Ifremer, Pointe Fort 97231 Le Robert, Martinique (FWI), E-mail lreynal@ifremer.fr

²IRD, centre de Brest, BP 70, 29280 Plouzané

³Ifremer, Pointe Fort 97231 Le Robert, Martinique (FWI)

Current use of moored Fish Aggregating Devices (FAD) presents the twofold drawback of encouraging the catching of juvenile fish and of blue marlin (*Makaira nigricans*) for which the International Commission for the Conservation of Atlantic Tunas (ICCAT) recommends a reduction in catches. To attempt to find solutions to these problems, a description of FAD fishing in Martinique was carried out via surveys during 2004 and 2005. A comparison of the catches was performed according to the location of the FAD and the time of fishing. The variation in the fishing compared to assessments made between 1998 and 2003 is also described. Analysing these data shows that over a few years yellowfin tuna (*Thunnus albacares*) has become the main species caught around FAD (50%). This species, along with blue marlin, accounts for 85% of landings. However, the number of blackfin tuna (*Thunnus atlanticus*) caught does not seem to have progressed, whereas this species makes up the majority of the biomass aggregating around these devices. Given the current state of knowledge about this species, it would seem that FAD near the coast are necessary in order to favour the fishing of adult blackfin tuna, whereas for yellowfin tuna, the best yields are obtained with devices further from the coast.

FISHING EFFORT AND PRODUCTION OF FISHING ASSOCIATED WITH MOORED FADS IN MARTINIQUE ESTIMATION BY PHONE SURVEYS

L. Reynal, L. Nelson, J.J. Rivoalen, and A. Lagin

Ifremer, Pointe Fort 97231 Le Robert, Martinique (FWI), E-mail lreyna@ifremer.fr

In order to estimate at an island scale the capture made by the emergent FADs fishing, two types of phone surveys have been realised. First, weekly surveys have been made during two years from voluntary FADs fishermen, on two different areas of Martinique. From these surveys, the numerical and ponderal capture per species has been detailed. The seasonality of the landings is described and shows the periods where low yield can force fishermen to abandon the FADs and go back to exploit the insular shelf resources. Length frequencies of captures, in particular of blue marlin (*Makaira nigricans*) are established with the estimation of individual weight declared by professional fishermen. The extrapolation to the whole fishery of Martinique has been made with a random sample of 10 percent of the fishing fleet. This survey also gives the proportion of boat fishing around FADs.

MANAGEMENT OF MOORED FISHING AGGREGATING DEVICE (FADS) IN THE LESSER ANTILLES: A BIO-ECONOMIC APPROACH

Oliver Guyader¹, Lionel Reynal², and Nicolas Diaz²

¹French Research Institute for the Exploitation of the Sea, Ifremer, centre de Brest, BP70, 29280 Plouzane, France, E-mail olivier.guyader@ifremer.fr

²French Research Institute for the Exploitation of the Sea, Ifremer, Pointe Fort, 97231 Le Robert, Martinique (FWI)

³Boyer, 97129 Lamentin, Guadeloupe (FWI)

The objective of this paper is to analyse the biological and economic implications of different management and funding regimes (private, public, collective) of the moored fishing aggregating devices (FADs). To consider this issue, a simple model of the commercial exploitation of a pelagic resource in a given area is developed to illustrate the potential effects of fishermen congestion around FADs and the biological interactions between the devices. Sensitivity analysis on the control variables of the model—the number of fishing unit and the number of FADs in the fishery—provide results on the level of profit and rent for the individual fisherman and for the total fleet. It illustrates the risk of rent dissipation in the case of mismanagement of the FADs as well as overcapacity in the fleet. Empirical evidence from a selection of fisheries in Martinique and Guadeloupe is used to discuss the assumptions and the results of the model.

CHALLENGES FOR THE MANAGEMENT OF AN EXPANDING SHARK FISHERY, WITH HIGH UNCERTAINTIES TOWARDS NEW CONSERVATION POLICIES IN THE SAN ANDRES, PROVIDENCIA AND SANTA CATALINA ARCHIPELAGO, COLOMBIA

Carlos Ballesteros and Erick Castro Gonzalez

Secretaría de Agricultura y Pesca, Av. Newball, Edificio Coral Palace, 2^{do} piso, Archipiélago de San Andrés, Providencia y Santa Catalina, Colombia, E-mail ballesteros.carlos@gmail.com

For over 20 years the Archipelago has held a strong fishing pressure at an industrial level centered principally on the extraction of the spiny lobster, queen conch and demersal fishes (snappers and groupers). However, in the last 5 years a new fishery has emerged targeting shark species, but unfortunately it has not been monitored. This study documents for the first time this shark fishery and established that 13 species of these elasmobranchs were captured; the majority included in the red list of the IUCN under different risk categories. Only one species, *Carcharhinus perezii*, makes up the majority of the fishery, representing nearly 68% of all sharks captured. Thus, *C. perezii* is vulnerable to overfishing, a condition that is accentuated with the high proportion of juveniles that are caught. The shark fleet operates over different areas in the north of the Archipelago, with a large part of the fishing effort inside a recently implemented system of marine protected areas of multiple use. Shark fishing occurs over zones where industrial fishing is not actually permitted, frequently affecting the coral habitat because of the use of

destructive fishing gear. Also, there exists a high level of uncertainty about the population ecology of the sharks caught and the effects that fishing of these top predators has on the trophic interactions in the ecosystem. Under these circumstances, local fisheries managers face true challenges in order to obtain an adequate management of this expanding fishery.

IMPACT OF ANNUAL AGGREGATIONS OF WHALE SHARK (*RHINCODON TYPUS*) ON THE NORTH AND NORTHEAST COMMUNITIES OF THE YUCATAN PENINSULA

Jaime González-Cano, Rafael De la Parra Venegas, Juan Pérez RAMÍREZ, Francisco Remolina Suárez, and Montserrat Trigo Mendoza

Comisión Nacional de Áreas Naturales Protegidas (CONANP). Venado No. 71, SM 20, Mz.18 C.P. 77500, Cancún, Q. R. México, E-mail jgonzalez@conanp.gob.mx

In just 3 years the lifestyle of communities on the north and northeast coast of the Yucatan Peninsula, Mexico has changed dramatically due to the occurrence of whale sharks in the area. What used to be a fish of no economic importance has become a factor of additional income to the populations of Holbox, Isla Mujeres and Cancun. This species has become the center of tourist activity in the Holbox area because the community is located at the closest site for the observation and swimming near the whale sharks. Data and statistics are presented to understand this phenomena which shows changes that have taken place within the communities and joint actions taken by both inhabitants of the community and authorities. Also presented are the results of a research project designed to learn more of the biology and the population dynamics of whale sharks as well as to evaluate the best strategies for the protection and conservation of the species. The results show that benefits could be achieved with compliance to the measures and regulations which have been designed. Although whale sharks are a transboundary species and its conservation depends on the efforts of many countries, the results presented here show the actions that could be achieved locally in a global effort for the conservation of the species.